Pigs, hogs or boars (suids) were not the subjects I thought to research during my PhD before I started, but I definitely fell in love with them during the journey. The same applies for Africa, though I have had the dream of working with something related to the wildlife of Africa since my childhood. In the end I was able to combine them with the second secret dream, being a palaeontologist in Finland.

In this thesis I have investigated the peculiar case of the Plio-Pleistocene African suids, which show shifting from omnivorous diet to grazing in three different lineages. I have conducted experimental work on dental wear by different food items with a mechanical masticator. My work also provides insights for abundances of the Turkana Basin suids in relation to climate changes in the Plio-Pleistocene and identifying a relationship between dental topography and diet preferences in present-day suids and applying the results for the extinct suids.

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JANINA RANNIKKO

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Adaptations of the Turkana Basin pigs (Suidae) to changing environments in the Plio-Pleistocene: tooth wear, diets and habitats

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ACADEMIC DISSERTATION
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"When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, nearly in the same way as when we look at any great mechanical invention as the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become!"

— Charles Darwin, On the Origin of Species

Rannikko, J. 2019. *Adaptations of the Turkana Basin pigs (Suidae) to changing environments in the Plio-Pleistocene: tooth wear, diets and habitats*. Painosalama, Turku. 51 pages, 6 figures.

Abstract

This thesis focuses on experimental dental wear research and the palaeoecology of suids (Mammalia: Suoidea, pigs) of the late Miocene to Pleistocene (ca. 8-0.7 Ma) Turkana Basin, situated in present-day northern Kenya and southern Ethiopia.

Suids are non-ruminating even-toed ungulates. Most of the present-day suids are omnivorous, medium-sized, and inhabit forest or dense vegetation environments. An exception is the warthog in Africa, which is adapted to an open environment and mainly consumes grasses. What seems to be an exception today, appeared more commonly in the past. During the Plio-Pleistocene at least three different dominant suid genera within two different subfamilies in Africa (*Notochoerus*, *Metridiochoerus* and *Kolpochoerus*) consequently adapted towards grass-eating. Isotope studies from enamel have demonstrated a strong gradual shift from a mixed diet towards grazing in all these genera. In addition, the molars of the Plio-Pleistocene African suids became more hypsodont (i.e., higher crowned) and increased the number of cusp pairs. Similar adaptations have been observed in other mammals such as horses already in the Miocene (23-5.3 Ma), when tropical grasses using the C4 photosynthetic pathway started to spread.

Suids in the Plio-Pleistocene Turkana Basin lived in the same environments as early hominins. An omnivorous lifestyle and bunodont cheek tooth morphology describes both groups, but during the Plio-Pleistocene the suids rapidly evolved towards species adapted to abrasive food items, while hominins retained their bunodont tooth morphology.

To better understand relationships between diets and dental wear patterns, an experimental dental wear study with a mechanical chewing machine was conducted. The aim was to investigate dental wear and enamel microwear patterns generated by diets with different amounts of abrasive particles. In the experiment, microwear patterns could not be distinguished between graze and browse diets, but the wear rate was higher in the grass diet than in the browse diet. The overall ranking of tooth wear rate from the highest to the lowest was: grass-rice-sand, grass-rice, grass, lucerne (browse) and attrition (chewing without food material). Diet including sand grains caused distinctly heavy damage on the teeth.

In addition to the study of the fundamental dental wear, this thesis focuses on the relative abundance and diet preferences of the Turkana Basin suids. In the second study the relative abundance of four suid genera in the Turkana Basin from the late Miocene (ca. 8 Ma) to the late Pleistocene (ca. 0.7 Ma) was investigated in relation to the changing environment. The peak abundances of the different genera consequently interplay and did not overlap. In addition, the peak specialisation of species to grazing did not occur at the same time, while species inhabiting both closed and open environments were always present, although in different proportions. The mostly unimodal patterns of the relative abundances, and the

fact that the peak times of the genera were not overlapping, suggest that each genera had its own time of success in the Turkana Basin area.

Finally, the dental surface topography of extant suids and African fossil suids was analysed to link the dental topography to specific diet preferences. Diets of the Plio-Pleistocene Turkana Basin suids were examined in relation to the present-day suids and Miocene suids using dental surface topography analyses. The two most herbivorous extant suids, warthogs and forest hogs, showed different dental topography as compared to other omnivorous suids (wild boars, bushpigs and babirusas). In addition, the more generalist wild boar was distinguished from the tropical forest species (bushpigs and babirusas) by higher occlusal patch count. In terms of their dental topography, two of the extinct Turkana Basin suids appeared the most similar to the warthog, and two had similarities with both the warthog and the omnivorous suids.

The results of this thesis extend scientific knowledge about the palaeoecology of the Turkana Basin Plio-Pleistocene suids, using the most extensive fossil database of the Turkana Basin as well as novel dental analysis methods: dental topography analyses were used extensively for the first time for suids and the chewing machine experiments were unique at the time in dental wear research.

Tiivistelmä

Tämä väitöskirja keskittyy kokeelliseen hampaiden kulumistutkimukseen sekä nykyisen Kenian pohjoisosissa ja Etiopian eteläosissa sijaitsevan Turkanan altaan alueella esiintyneiden sikojen paleoekologiaan mioseenin lopulta pleistoseeniin (noin 8-0.07 Ma).

Suurin osa nykyisin elävistä sioista (Suidae, Mammalia) on kaikkiruokaisia, keskikokoisia, metsässä tai muutoin tiheän kasvillisuuden seassa eläviä sorkkaeläimiä. Pahkasika (*Phacochoerus*) on kuitenkin poikkeus; pahkasiat elävät Afrikan avoimilla heinätasangoilla ja käyttävät pääravintonaan heinää. Plio-pleistoseenin aikaisessa Afrikassa oli kolme eri sikalinjaa (*Nyanzachoerus-Notochoerus*, *Kolpochoerus* ja *Metridiochoerus*), joiden arvellaan sopeutuneen avoimiin ympäristöihin ja heinän hyödyntämiseen ravintona pahkasian tapaan. Isotooppianalyysit hampaiden kiilteestä ovat osoittaneet, että kaikki nämä sikalinjat siirtyivät vähitellen sekaruokavaliosta kohti heinänsyöntiä. Myös niiden poskihampaiden kruunun korkeus kasvoi ja hammasnystyjen määrä lisääntyi. Samanlaisia muutoksia on havaittu muissakin nisäkäsryhmissä jo mioseenin (23–5.3 Ma) aikana, jolloin trooppiset C4-fotosynteesiä käyttävät heinät alkoivat levitä.

Muinaiset siat ja ihmisten sukulaiset asuivat samoissa elinympäristöissä Turkanan altaan alueella plio-pleistoseenin aikana. Sekasyönti ja hampaiden muoto yhdistävät monia sika- ja ihmislajeja. Afrikassa siat kuitenkin kehittyivät plio-pleistoseenin aikana nopeasti lajeiksi, jotka olivat sopeutuneet syömään kuluttavaa ruokaa.

Väitöskirjatutkimuksessani tein kokeellista tutkimusta mekaanisella purulaitteella tutkiakseni erilaisten ruokavalioiden aiheuttamaa hampaiden kokonaiskulumista ja mikrokuvioinnin syntyä. Mikroskooppiset kulumisjäljet eivät olleet merkitsevästi erilaista heinän ja lehtevän ruokavalion välillä, mutta heinä aiheutti suuremman hampaan kokonaiskulumisen. Sen lisäksi hiekkaa sisältävä ruokavalio kulutti hammasta paljon.

Hampaankulumistutkimuksen lisäksi keskityin Turkanan alueen sikojen ekologiaan. Toisessa tutkimuksessani perehdyin eri sikalajien runsauteen eri aikoina myöhäis-mioseenin ja pleistoseenin välillä Turkanan altaan alueella. Eri sikalajit olivat runsaimmillaan eri aikoina. Lisäksi hyvin pitkälle kehittyneet lajit eivät esiintyneet samaan aikaan. Sen sijaan sekä tiheää kasvillisuutta että avointa ympäristöä suosivia lajeja eli koko ajan samoilla alueilla.

Kolmanneksi tutkin erilaisia ruokia syövien nykyisten sikojen hampaiden pinnan topografiaa. Vertailin myös nykyisten sikojen hampaiden pinnan topografiaa Turkanan altaan muinaisten sikojen hampaiden pinnan topografiaan päätelläkseni niiden ruokavalioita. Pääosin kasviruokavaliota käyttävät siat, pahkasika ja metsäkarju, eroavat hampaan pinnan topografialtaan muista sekasyöjä sioista (villisika, pensassika ja hirvisika). Lisäksi, villisika voidaan erottaa muista sekasyöjä sioista (pensassika ja hirvisika) hampaan pinnan monimutkaisuuden avulla. Kaksi Turkanan altaan sikalajia muistuttivat hampaan pinnan topografialtaan eniten pahkasikaa, ja toiset kaksi muistuttivat osin pahkasikaa sekä osin muita sekasyöjä sikoja. Tämä tukee aikaisempien tutkimusten tuloksia siitä, että Turkanan altaan alueella on ollut hyvin vaihtelevia elinympäristöjä viimeisen 4 miljoonan vuoden aikana.

Tulokseni lisäävät tietoa Turkanan altaan plio-pleistoseenin sikojen paleoekologiasta, lisäksi tässä tutkimuksessa hampaan pinnan

topografia-analyysejä käytettiin ensimmäistä kertaa laajasti sikoihin. Purulaitekokeet osoittavat mikrokulumisen monimutkaisuuden sekä useamman menetelmän tarpeellisuuden paleoekologisissa tutkimuksissa.

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Contents

List of original publications

I. Karme, A. J.*, Rannikko, J. C.*, Kallonen, A. P., Clauss, M. and Fortelius, H. L. M. 2016. Mechanical modelling of tooth wear. Journal of the Royal Society Interface 13 (120), 20160399.

II. Rannikko, J., Žliobaité, I. and Fortelius, M. 2017. Relative abundances and palaeoecology of four suid genera in the Turkana Basin, Kenya, during the late Miocene to Pleistocene, Palaeogeography, Palaeoclimatology, Palaeoecology 487, 187-193.

III. Rannikko, J., Adhikari, H. Karme, A., Žliobaité, I. and Fortelius, M. The case of the grazing suids in the Plio-Pleistocene Turkana Basin: 3D dental topography in relation to diet in extant and fossil suids. In review: Journal of Morphology.

*Co-first authors
The publications are referred to in the text by their roman numerals.

Author's (J.R.) contribution to the publications

I. *Study design*: A.J.K., M.F., M.C. and **J.R.**
Material collection: **J.R**. and A.J.K.
Analyses: **J.R.**, A.J.K. and A.P.K.
Interpretation: **J.R.** A.J.K. and M.F.
Preparation of manuscript: **J.R.** and A.J.K. with comments and corrections from M.F., M.C. and A.P.K.

II. *Study design*: **J.R.**, I.Z. and M.F.
Material collection: **J.R.**
Analyses: **J.R.**
Interpretation: **J.R.**, I.Z. and M.F.
Preparation of manuscript: **J.R.** with comments and corrections from M.F and I.Z.

III. *Study design*: **J.R.**, A.K., M.F. and I.Z.
Material collection: **J.R.**
Analyses: **J.R.**, H.A. and A.K.
Interpretation: **J.R.**, M.F., I.Z. and A.K.
Preparation of manuscript: **J.R.** with comments and corrections from H.A., M.F, I.Z. and A.K.

Abbreviations

CT	Computed Tomography	OPC	Orientation Patch Count
DNE	Dirichlet Normal Energy	OPCR	Orientation Patch Count Rotated
GIS	Geographic Information System	RFI	Relief Index
Kyr	Thousand years	SEM	Scanning Electron Microscope
Ma	Million years ago	SHI	Sharpness Index
MSS	Mean Surface Slope	2D	Two Dimensional
Myr	Million years	3D	Three Dimensional

List of figures

1 Introduction

1.1 The rapid evolution of the grazing suids in hominin environments of the Plio-Pleistocene eastern Africa

Suids (Suidae, Mammalia), otherwise known as pigs, can be characterised as non-ruminating even-toed ungulates that have low and round-cusped (bunodont) teeth and are typically omnivorous (consume variety of plant and animal material) forest dwellers. Although many of the suids, whether extant or extinct, fall into the abovementioned categories, some exceptions can be found in the history of the suids, which started in the Eocene (56-33.9 Ma) (Harris and White 1979, Hunter and Fortelius 1994, Ducrocq et al. 1998). For example some of the listriodontine suids from the Miocene (23-5.3 Ma) have been classified as browsers, based on their molar morphology with two transverse ridges on the occlusal surface (bilophodont), enamel microwear patterns, and isotope studies (Quade et al. 1994, Hunter and Fortelius 1994, Cerling et al. 1997, Morales and Pickford 2003).

Among the present-day suids, the warthog (*Phacochoerus* spp.) is special: it lives in the open savanna and mostly consumes grasses (Ewer 1958, Field 1970, Treydte et al. 2006). In the Plio-Pleistocene (5.3-0.01 Ma) Africa, there were three different lineages of suids who exhibited similar morphological adaptations as the warthog (Harris and White 1979). In addition, isotope studies have suggested that these suids consumed grasses (Harris and Cerling 2002, Cerling et al. 2015). The most notable adaptations in their morphology were to increase the crown height (hypsodonty) of the teeth and to add extra cusp pairs in the third molars (horizontally elongated i.e. horizodonty [Žliobaitė et al. 2016]) (Harris and White 1979).

Suids went through rapid evolutionary changes during the Plio-Pleistocene in Africa in the same environments that early hominins lived in (White and Harris 1977, Cooke 1978, White 1995, Bobe and Behrensmeyer 2004). At the same time, aridity increased in eastern Africa and open woody grassland taxa took over the forest and woodland taxa (Wynn 2004, Bobe et al. 2002, Harris and Cerling 2002, Bishop et al. 2006, Bonnefille 2010).

The rapid evolution of the African suids has created problems: there is a significant number of synonyms and confusion in the relationships between the different genera and species (White and Harris 1977, Cooke 1978, Harris and White 1979, Pickford 2006). On the other hand, the rapid evolution of the suids and large collections of suid teeth fossils created an opportunity to use the suids as biostratigraphical indicators (Cooke and Maglio 1972). Detailed studies of suid palaeoecology can reveal conditions and changes in the environments of the Plio-Pleistocene suids and hominins.

Understanding the Plio-Pleistocene suids will help us not only to better reconstruct the palaeoenvironments, but also to aid us in the improved understanding of evolutionary processes and the environmental context of early humans.

1.2 Teeth as a proxy for diet and environment

Teeth are an important part of this thesis. The rapid evolution and specialisation of the Plio-Pleistocene suids are best seen from their molars (Harris and White 1979, Kullmer 1999). Moreover, teeth can reveal the animal's diet, ecology, and environment (Walker et al. 1978, Solounias et al. 1988, Quade et al. 1994, Boisserie et al. 2005, Evans 2013, Souron et al. 2014, Saarinen and Karme 2017).

Teeth are essential tools for animals

because they act as an interface between the animals and their environments that enables the animals to obtain energy from the surroundings. Dental morphology among all animals is diverse because they have adapted to consume different foods (Ungar 2010). Different environments accommodate various diet categories in different proportions (Gordon and Prins 2007). Therefore, adaptations to different diets allow many herbivores to share the same environment by fitting in different ecological niches.

Depending on herbivores' preferred diets, they need different types of teeth because of the different mechanical properties of the plants (Cuvier 1827, Fortelius 1985, Popowics and Fortelius 1997, Strait 1997, Elgart-Berry 2004, Massey et al. 2009, Rabenold and Pearson 2011, Strömberg et al. 2016). Sharp enamel edges are effective for the browse diet (shoots, twigs, leaves of trees and shrubs etc.), whereas the graze diet (grasses) needs different grinding capability. While teeth wear continuously in the chewing process, the tooth wear also maintains necessary shape for continuous use (Fortelius and Solounias 2000).

The dental adaptations of the herbivores to different diets make their teeth valuable research material for palaeoecological and -environmental studies. This is because we can reconstruct diet from dental morphology. In addition, teeth tend to preserve well in the fossil record as compared to other body parts, because the enamel of the teeth is a mineralised and highly durable material (Lawn et al. 2010), that must endure daily mechanical usage for a lifetime.

The most common grouping of ungulates divides them into three dietary categories: browsers, mixed-feeders, and grazers (Hofmann and Stuart 1972, Janis and Ehrhardt 1988, Solounias et al. 1994). While ungulates in any category can be found in a variety of environments, higher proportions of browsers can be found in closed forests than in open grasslands, and grazers vice versa (Bodmer and Ward 2006). Other common dietary categories are frugivores (fruit eaters), folivores (leaf eaters) and insectivores (insect eaters) (Kay 1975, Teaford et al. 1996). Suids do not fit perfectly into any of the diet categories. They are often described as omnivores that are capable of consuming a variety of plant and animal material, such as grasses, fruits, tubers, meat, and insects (Ewer 1958, Ewer 1970, Ghlieri et al. 1982, Leus et al. 1992, Leus 1994). Their omnivorous habits are possibly like those of early hominins (Ungar et al. 2006). However, wild boar is perhaps the only true generalist or opportunist species among the suids. Warthogs prefer grazing, and bushpigs and babirusas consume large amounts of fruits (Field and Laws 1970, Skinner et al. 1976, Ghlieri et al 1982, Tulung et al. 2013). Their diets are also linked to the environment where they live; warthogs live in the open savanna, and bushpigs and babirusas live in the tropical forests (Melletti and Meijaard 2017).

To understand the link between teeth, diets, and environments, we must understand how they relate quantitatively to each other. The shape and structure of an unworn tooth can reveal the dietary adaptation of an animal, because the initial shape is the result of a long adaptation to prevalent conditions (Kay 1975, Yamashita 1998, Evans and Sanson 2003, Lucas et al. 2008). Therefore, by analysing patterns of the tooth shape, we can predict the environmental conditions to which those species are adapted. For example, tooth crown height, hypsodonty, either alone or combined with lophedness, can predict precipitation (Fortelius et al. 2002, Eronen et al. 2010a, Eronen et al. 2010b, Liu et al. 2012, Fortelius

et al. 2016, Žliobaitė et al. 2016).

Worn teeth, on the other hand, are a product of using the teeth for chewing food. Thus, teeth can reveal what an animal has eaten during its life (Fortelius and Solounias 2000, Ungar and Williamson 2000). As teeth wear, they must retain an effective shape for as long as possible because they have only limited renewal capabilities after eruption. Therefore, tooth wear is a way to keep the teeth functional throughout the lifetime (Fortelius 1985). Mesowear analysis, dental surface topography analyses and microwear analysis have been used to study worn teeth in relation to diets (Walker et al. 1978, Fortelius and Solounias 2000, Ungar and Williamson 2000).

Mesowear analysis categorises ungulates into either grazers, graze-dominated mixed feeders, browse-dominated mixed feeders, or browsers. These categories are based on the shape of the cusps on the occlusal surface that is produced by attritive (tooth-to-tooth contact) and abrasive (tooth-to-food contact) wear (Fortelius and Solounias 2000, Kaiser and Fortelius 2003, Clauss et al. 2007, Hernesniemi et al. 2011, Butler et al. 2014). However, the original mesowear methodology has been tailored for specific dental morphologies and does not apply to suids directly. Derived mesowear analyses using angle measurements have been developed to measure the diet preferences of Proboscidea and Xenartha (Saarinen et al. 2015, Saarinen and Karme 2017). I have explored the possibility to use similar methods for suids such as Saarinen et al. (2015), but the complexity of the facets, which is mainly due to the vertical movements of the jaw, and the small size of the suid teeth compared to Proboscidean teeth made it too challenging to continue further within this doctoral thesis.

Dental surface topography analyses have become popular as three-dimensional (3D) scanning methods and digital measurement methods have become widely available, cheaper, and more efficient (M'Kirera and Ungar 2003, Ungar and M'Kirera 2003, Ungar 2004, Dennis et al. 2004, Boyer 2008, Bunn and Ungar 2009, Winchester et al. 2014, Pampush et al. 2016, Prufock et al 2016, Yamashita et al. 2016, Ungar et al. 2018). Compared to the traditional geometric morphometrics, 3D analysis methods measure the whole surface and are independent of landmarks (Ungar and Williamson 2000, Evans 2013). Dental topography analyses with measures like the relief index (ratio of 3D surface to 2D surface), mean surface slope and its derivatives, angularity and sharpness index, have been found to accurately identify different diets, for example frugivores and folivores, among primates (Boyer 2008, Ungar and M'Kirera 2003, Ungar et al. 2018). Other animal groups still lack comprehensive dental topography studies. Thus, I have used these methods for linking diets of extant suids to their dental topography and applied them for analysis on the Turkana Basin fossil suids.

As food items and items from the environment have direct contact with the surface of the tooth, they leave microscopic wear marks on the occlusal surface. Following these patterns, dental microwear analysis has been used to predict the foods consumed by the animals (Walker et al. 1978, Rensberger 1978). Commonly used dietary categories can be identified this way, since browsers tend to have pit-dominated microwear patterns and grazers scratch-dominated microwear patterns (Solounias et al. 1988, Solounias and Moelleken 1992, Mainland 2003). Grasses contain abrasive silica phytoliths, which leave striations on the enamel, while browsing includes more attrition and thus leaves a

different, less striated pattern. In primates frugivores tend to have more pits and folivores more scratches (Teaford and Walker 1984, Ungar 1996). Analysing the proportions of different marks, enables the reconstruction of the proportions of grass and browse in diets (Solounias et al. 1988, Mainland 2003). However, microwear can change quickly and might thus represent only a part of the diets. The rapid overwriting may also mask seasonal variation if the individuals under study have died during the same season (Teaford and Robinson 1989, Teaford and Oyen 1989, Rivals and Solounias 2007). The traditional microwear analysis is sensitive to observer errors, and the use of 2D images masks the depth dimension (Mihlbachler et al. 2012). In response to these challenges, microwear texture analysis has been introduced to reduce subjectivity and take advantage of the 3D surface of the tooth (Scott et al. 2006, Ungar et al. 2007, Ungar et al. 2008). I have used the traditional microwear analysis for experimental studies of tooth wear by diets with different abrasive content.

Chemical analyses are as relevant as physical analyses in the study of the diets (DeNiro and Epstein 1978, Cerling and Harris 1999, Boisserie et al. 2005). Chemical analyses reveal features that cannot be seen from the structure. Moreover, they are a source of diet information that is independent from the shape and wear analyses. Isotope analyses are often used for determining the trophic niche and diet preferences by measuring the nitrogen, carbon and oxygen isotope ratios (DeNiro and Epstein 1981, Kohn et al. 1996, Sponheimer and Lee-Thorp 1999, Cerling and Harris 1999). Carbon isotopes are especially informative when studying tropical herbivores because most tropical grasses use different photosynthesis type (C4) than most of the forest and woodland plants (C3) (Lee-Thorp et al. 2007, Cerling et al. 2015). The different pathways have dissimilar ratios between the carbon isotopes ^{13}C and ^{12}C ($\delta^{13}C$), because the pathways fractionate the carbon differently (Tieszen et al. 1983). When animals consume these plants, the isotopes end up in their bodies, and the ratio is locked in the mineralizing enamel (Tieszen et al. 1983). Thus, the animals' enamel reflects the $\delta^{13}C$ values of the plants they consume. Analysis of the isotopic composition of the enamel indicates the diet consumed during the growth of the teeth (Cerling et al. 1999, Cerling et al. 2003). I have not performed isotope analyses myself in my studies, but most of the knowledge about the diets of the Plio-Pleistocene Turkana Basin suids has been obtained by isotope analyses (Harris and Cerling 2002, Bishop et al. 2006, Braun et al. 2010, Cerling et al. 2015). Thus, I have used isotope results available in the literature.

1.3 Grazing and the evolution of grasslands

Isotope studies and the increasing hypsodonty and horizodonty of the third molars of the Plio-Pleistocene suids have suggested that they adapted to increased grass consumption (Harris and White 1979, Harris and Cerling 2002).

Today, grasslands cover around 40% of the land surface (Gibson 2009). Grazers are animals that use grass as their main food source. Depending on the study, animals whose diet consists of more than 75% or 90% grasses are defined as grazers (Janis 1990a, Mendoza et al. 2002). Grasses are demanding consumables because they have high silica content, thick and fibrous cell walls, and slowly digestible cellulose (Baker et al. 1959, Demment and Van Soest 1985, McNaughton et al. 1985). Grazing ruminants have proportionally larger masseter muscle, which relate to the greater chewing power needed to process grasses (Clauss et

al. 2008a). Furthermore, grasslands are wide and open, which enhance dust and grit intake while animals consume grasses (Damuth and Janis 2011, Jardine et al. 2012). However, the nutritional values of different grasses are variable, Paine et al. (2018) have demonstrated that circa 25% of the grass species they sampled from African savannas represent high quality resources in their respective habitats. Grasses also lack most of the toxic chemicals that dicotyledonous plants have (Coughenour 1985), therefore dedicated grazers do not need extensive physiological adaptations to neutralize toxins.

Most tropical grasses use the C4 photosynthesis pathway because it is more efficient than the C3 pathway in the high temperatures of the growing season with water stress and in conditions of more light (Teeri and Stowe 1976, Öztürk et al. 1981, Pearcy and Ehleringer 1984). The C4 pathway evolved after the C3 pathway, and it was only after 6 Ma when C4 grasses started to dominate some ecosystems, possibly because of decreasing atmospheric carbon dioxide (Cerling et al. 1993, Ehleringer and Monson 1993, Ehleringer et al. 1997, Cerling et al. 1998).

Retallack (1997) has pointed out that there was no single origin for grassland ecosystems. Evidence of grasses has already been found in the Cretaceous, but grasslands did not appear until the middle Miocene (Retallack 1997, Strömberg 2002, Strömberg 2011). Some taxa in the Great Plains of North America demonstrated adaptations to open habitats during the middle Miocene 18-15 Ma, and phytoliths have demonstrated that there were dominant grasslands in the Great Plains during 25-17 Ma. However, the spread of the vast C4 grasslands occurred only after 7-6 Ma (MacFadden and Hulbert 1988, Cerling et al. 1993, Retallack 1997, Strömberg 2002, Strömberg 2011).

In Asia, enamel isotopes have demonstrated that C4 grasses were present in China by the late Miocene (Passey et al. 2009, Arppe et al. 2015). Studies from the Siwalik sequence have revealed that C4 grasses began to emerge after 8.1 Ma, and grassy woodlands appeared in northern Pakistan by 7.4 Ma (Quade and Cerling 1995, Barry et al. 2002).

The middle Miocene locality Fort Ternan in Kenya, Africa, has provided evidence for a heterogeneous landscape with C3 grasslands (Cerling et al. 1997, Jacobs 1999). Evidence of C4 grasses has been found in the 9.4 Myr old Baringo Basin (Cerling 1992), but grasslands dominated by C4 grasses appeared around 5 Ma (Levin et al. 2004, Feakins et al. 2005). Strömberg (2011) has suggested that fully open grasslands were likely to be a late Miocene-Pliocene phenomenon.

The evolution of grasslands affected the Plio-Pleistocene suid evolution in Africa, although suids were rather late to shift to the C4-diet compared to groups like the Rhinocerotidae, Equidae and Bovidae (Cerling et al. 2015).

Today, only one suid, the warthog, has the adaptations to open grasslands and grazing (Ewer 1958). However, during the Plio-Pleistocene, several species of suids developed similar adaptions independently. The circumstances of these independent adaptations is the central unifying topic of this thesis.

1.4 Extant and fossil suids and their ecology

The present clade Suina includes two families: Suidae (pigs) and Tayassuidae (peccaries). The origin of both lineages is thought to be in Asia at the Eocene. Currently, three species of peccaries inhabit the New World, and 17

species of suids (though the species number in genus *Sus* is uncertain) inhabit the Old World (Melletti and Meijaard 2017). Extant suids have been assigned to six genera: *Babyrousa* (babirusas), *Phacochoerus* (warthogs), *Hylochoerus* (forest hogs), *Potamochoerus* (bushpigs), *Porcula* (pygmy hog) and *Sus* (wild boars and domestic pig) (Melletti and Meijaard 2017).

Present-day suids are well-known for their omnivorous and flexible lifestyle, which enables them to inhabit various environments and survive on a range of foods (Melletti and Meijaard 2017). Suids are characterised by their nasal disc and large, upward-curving canines. Most of the suid species, living and extinct, have bunodont teeth, which are well adapted for their omnivorous diet. Suid enamel is also specially folded around the cusps, which can be viewed as furrows or Furchen (Hünermann 1968). Most of the suids have central cusps between the main cusp pairs in their molars, which inhibits large trans-verse chewing motions. Thus, the chewing cycle is more vertical with a slight transverse component. The masticatory cycle of a miniature pig consists of jaw motion in all planes of space: the opening movement, the closing movement and, transverse and longitudinal movements in the closing position, which is usually reversed in every chew (Herring and Scapino 1973, Herring 1976). Based on molar morphology and the wear of canines, Ewer (1958) has suggested that the bushpig has a simple chopping jaw movement without marked longitudinal or transverse movement. On the other hand, warthogs and forest hogs have teeth that undergo extended transverse movements during their chewing cycle (Ewer 1958, Herring 1985).

Although many suids can be categorised as omnivores, there are some species that express adaptations in their dental characteristics towards the herbivorous diets of either browsing or grazing. Advanced listriodontines in the Miocene had high relief bilophodont dental morphology, which is associated with the browsing diet (Hunter and Fortelius 1994). In addition, isotope analyses have demonstrated that listriodontines were mainly consuming C3 plants (Quade et al. 1994, Cerling et al. 1997). Nowadays, the forest hog (*Hylochoerus meinerzthageni*) and the Chacoan peccary (*Catagonus wagneri*) have almost lophed cusp pairs, although these are not as developed as in some listriodontines (Herring 1985, Ewer 1970). In contrast, warthogs can be categorised as grazers (Ewer 1958, Field 1970, Clauss et al. 2008b), and several species from Plio-Pleistocene Africa have similar adaptations towards grazing in their skulls and dentition as warthogs (Harris and White 1979).

1.4.1 Extant suids outside sub-Saharan Africa

Babirusas (*Babyrousa* spp.) live in the tropical islands of Indonesia (Long 2003). They are almost hairless, and the males have peculiar canines protruding through their skin (Melletti and Meijaard 2017). They prefer a closed rainforest environment. Babirusas are omnivorous, but consume large amounts of fruits (Leus et al. 1992, Leus 1994, Tulung et al 2013). They do not have strong rooting behaviour because their nose lacks a large rostral bone that makes efficient rooting possible (Leus et al. 1992). The body weight of babirusa can be from 60 to over 100 kg (Melletti and Meijaard 2017). The molars of the babirusa are bunodont, low crowned (Fig. 1A) and strong enough to crack various seeds and nuts (Leus et al. 1992).

The pygmy hog (*Porcula salvania*) is critically endangered and is found only in

protected areas in northeast India (Blouch 2014). As the name implies, the pygmy hog is the smallest of the extant suids. Its body mass is about 7-9 kg (Meijaard and Melletti 2017). Pygmy hog inhabits tall grasslands near rivers, where it mostly hides and builds nests (Melletti and Meijaard 2017). Pygmy hog is omnivorous (Deka et al. 2009).

All other species in Eurasia belong to the genus *Sus*. The most widely spread is the wild boar (*Sus scrofa*), which is encountered throughout Eurasia, from Portugal to Japan (separation to several species by spatial range has been suggested [Groves and Grupp 2011]). The key factors for the wide distribution of the wild boar are flexibility with habitat and diet as well as a high reproduction rate (Sáez-Royuela and Telleria 1986, Schley and Roper 2003, Segura et al. 2014, Frauendorf et al. 2016). The body weight of *Sus* species range from 20 to 320 kg (Melletti and Meijaard 2017). The wild boar is also the ancestor of domestic pigs. It has bunodont cheek teeth with highly folded enamel and has an increased number of cusps in the third molars (Fig. 1C). All other *Sus* species are restricted to islands of Southeast Asia. The *Sus* species can be found in various environments, although many species prefer forests (Segura et al. 2014). Some endangered species in Southeast Asia are found only in high altitude forests, where humans are mostly absent. Others take advantage of croplands and turn their normally diurnal activity to nocturnal crop raiding (Semiadi and Meijaard 2006, Luskin et al. 2014).

1.4.2 Extant suids in sub-Saharan Africa

In present-day Africa, there are three genera of wild suids: *Phacochoerus* (warthogs), *Potamochoerus* (bushpigs), and *Hylochoerus* (forest hogs). Warthogs (*Phacochoerus africanus* and *Phacochoerus aethiopicus*) are special among living suids because they are adapted to an open landscape and grazing diet (Ewer 1958). They are highly selective feeders; they pluck short grass carefully from the ground and favour short grasslands, although they are also powerful diggers (Ewer 1958, Field 1970, Field and Laws 1970, Jarman 1972, Hirst 1973, Treydte et al. 2006). Enamel isotopes have also indicated evidence of grass consumption (Harris and Cerling 2002). In addition, warthogs digest fibre more efficiently than other wild suids and peccaries (Clauss et al. 2008b). Warthogs' body masses range from 45 to 105 kg (Melletti and Meijaard 2017). The hypsodont molars of the warthog are especially interesting. The third molars often consist of over fifteen columnar cusps (Fig. 1E). The roots of the third molars have delayed maturation, which enable the third molars to grow almost continuously while in use (Spinage and Jolly 1974). Old individuals usually have their second molars worn out and only have the third molars left. The occlusal relief is mainly low, reflecting wear by abrasion.

Bushpigs (*Potamochoerus larvatus* and *Potamochoerus porcus*) are rooting species that prefer closed environments (Ewer 1958, Skinner et al. 1976, Breytenbach and Skinner 1982, Ghiglieri 1982, Vercammen et al. 1993, Souron et al. 2014). *Potamochoerus larvatus* inhabits eastern and southern parts of Africa, whereas *P. porcus* (also called the red river hog) is found in western and central Africa, although they have overlapping ranges in some areas (Vercammen et al. 1993, Meijaard and Melletti 2017). Body masses of the bushpigs range from 45 to 115 kg (Melletti and Meijaard 2017). *Potamochoerus porcus* has powerful jaws capable of crushing seeds (Herring 1985, Beaune et al. 2012). Breytenbach and Skinner (1982) described *P. porcus* as an omnivore in a broad sense, but with preference to some

food items like fruits. According to dental microwear texture analysis, these two species are very similar in their omnivorous diets (Souron et al. 2014). They have bunodont low-crowned cheek teeth (Fig 1B).

The forest hog (*Hylochoerus meinertzhageni*) inhabits thick vegetation areas from mountain bamboo forests to bushlands (d'Huart 1993, Melletti and Meijaard 2017). Body masses of the forest hogs range from 100 to 275 kg (Melletti and Meijaard 2017). Forest hogs have been observed to feed on both grasses and herbaceous plants (Ewer 1970, Kingdon 1979, Harris and Cerling 2002, Cerling and Viehl 2004). Consumption of grasses has been observed to increase during the wet seasons (Cerling and Viehl 2004). Dental microwear texture analysis has suggested that the forest hog is an herbivorous mixed-feeder (Souron et al. 2014). However, insects and their larvae might also be an important part of its diet (Ewer 1970). Forest hogs do not have strong rooting behaviour (Ewer 1970). The molars of the forest hog are special among extant suids. The crown is moderately high and almost lophodont: the cusp pairs form ridge-like structures horizontally over the occlusal surface. The cusps are not tightly packed, which makes the relief high. Extra cusplets are few and arranged into longitudinal valleys between the crests (Herring 1985) (Fig. 1D).

1.4.3 Plio-Pleistocene suids of the Turkana Basin

Although *Phacochoerus* is special among living suids in that it is a grazer, four African suid genera during the late Miocene to early Pleistocene had adaptations in their dentition that were similar to *Phacochoerus* (Harris and White 1979). *Nyanzachoerus* and *Notochoerus* were tetraconodontines, a now extinct suid subfamily famous for their large premolars (Van der Made 1998). *Notochoerus* was possibly a direct descendant of the *Nyanzachoerus* lineage (White and Harris 1977, Cooke 1978). *Kolpochoerus* and *Metridiochoerus* were part of the Suinae subfamily, like all present-day suids. The ancestry of *Kolpochoerus* and *Metridiochoerus* has been suggested to be in the Eurasian *Propotamochoerus* (via *Dasychoerus* and *Potamochoeroides* respectively), which migrated to Africa in the late Miocene or early Pliocene (Pickford 2012, Pickford and Obada 2016). *Hylochoerus* is argued to be a descendant of the *Kolpochoerus* lineage, and the extant warthog (*Phacochoerus*) is argued to be a descendant of the *Metridiochoerus* lineage (White and Harris 1977, Cooke 1978, Harris and White 1979, Kullmer 1999) (Fig. 2).

Tetraconodontine suids were the most

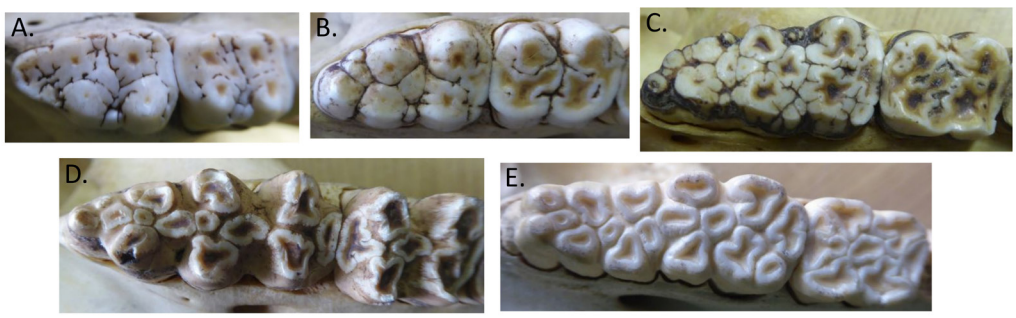

Figure 1. Moderately worn third (on the left) and second (on the right) upper molars of extant suids. A) *Babyrousa* sp. B) *Potamochoerus* sp. C) *Sus scrofa* D) *Hylochoerus meinerzthageni E) Phacochoerus africanus*. Photos by J. Rannikko.

abundant suids in the latest Miocene and early Pliocene in eastern Africa. Several *Nyanzachoerus* species have been named throughout eastern Africa (Boisserie et al. 2014). In the Turkana Basin database the nyanzachoeres are referred as *N. kanamensis*, *N. kanamensis australis*, *N. pattersoni*, *N. syrticus* and *N. tulotos*. Most of them had rather bunodont and low crowned molars, but later species, especially *N. kanamensis* did have an extra cusp pair in their third molars (Harris and White 1979). Isotope studies have suggested that the Miocene species consumed mainly C3 plants, but the early Pliocene species shifted to mixed C3-C4 diets (Fig. 3). The average body mass for *Nyanzchoerus kanamensis* has been estimated to be 255 kg (pers. comm. Juha Saarinen, based on the dimensions of the second molars, after Janis 1990b). *Nyanzachoerus/ Notochoerus jaegeri* has been thought to be the linking species between the two genera (Harris and White 1979, Van Der Made 1998, Bishop 2010). It had larger and more hypsodont molars than other nyanzachoeres. Reda et al (2017) provided the first detailed description of the skull of *Ny./No. jaegeri*, and concluded that it is more similar to *Ny. kanamensis* than to *No. euilus* and thus should be placed in genus *Nyanzachoerus*.

Notochoerus species were larger than nyanzachoeres and their third molars had more than one extra cusp pair (Fig. 4A and 4C) (Harris and White 1979). The Turkana Basin database includes three species of *Notochoerus*: *N. euilus*, *N. capensis* (only three specimens) and *N. scotti*. Post-cranial analysis from the earliest one, *Notochoerus euilus*, suggested that the species was living in an intermediate environment between a savanna and a forest (Bishop 1999). The last and most specialised

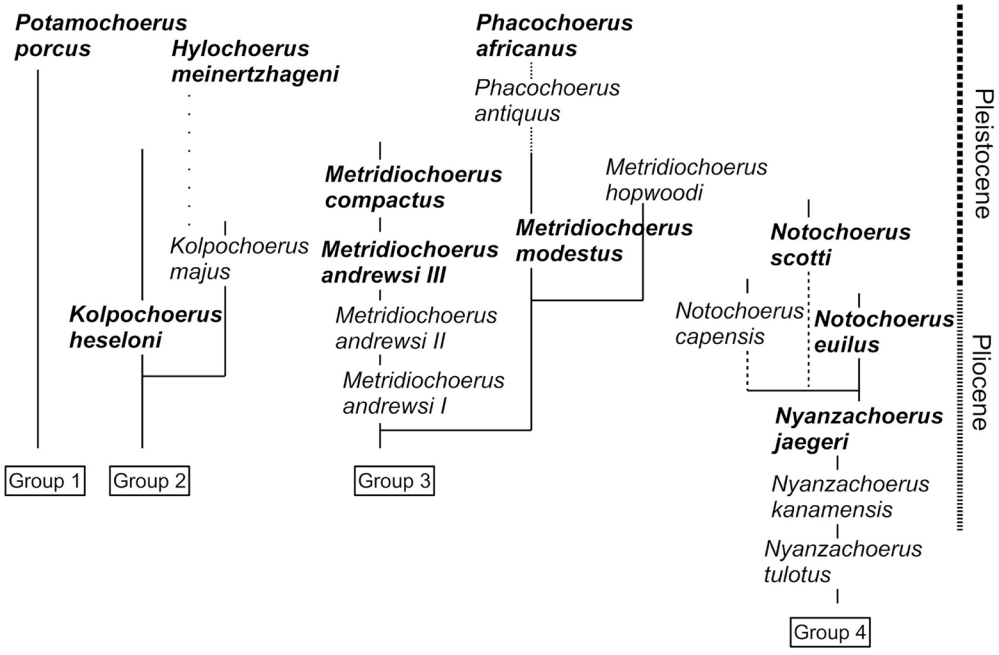

Figure 2. Reduced phylogeny of Cenozoic African suids, after White and Harris (1977) and Cooke (1978). Additional species have been found and named, but are not included here for simplicity. Species that have been mentioned in the research articles included in this thesis are in bold.

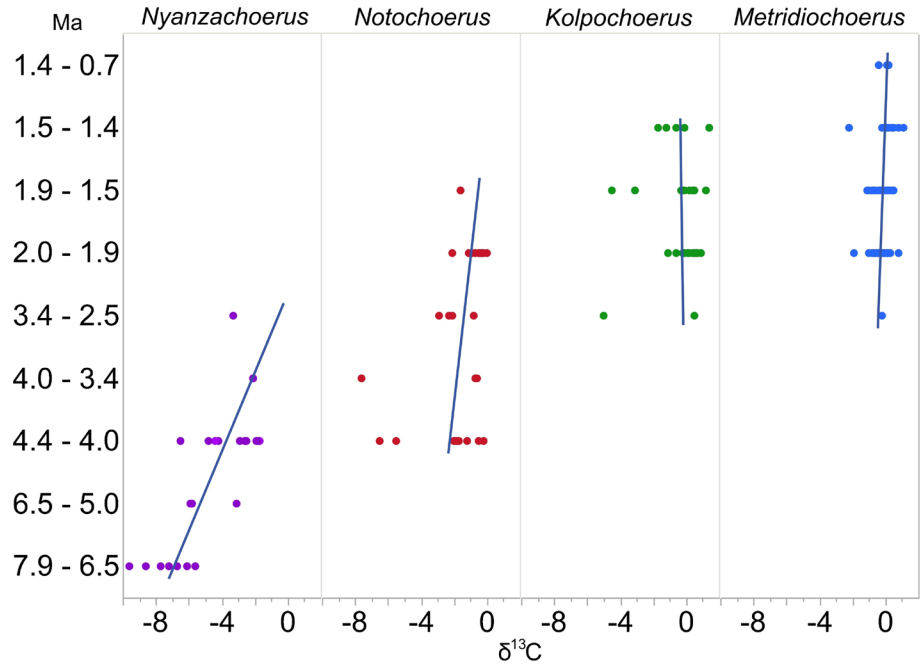

Figure 3. This figure depicts $\delta^{13}C$ values from *Nyanzachoerus*, *Notochoerus*, *Kolpochoerus* and *Metridiochoerus* specimens from the Turkana Basin from 7.9 to 0.7 Ma. Higher $\delta^{13}C$ indicates more C4 plants in their diet. Values are from Harris and Cerling (2002), Braun et al. (2010) and Cerling et al. (2015).

of notochoeres in the Turkana Basin was *N. scotti*. Its third molars were the largest among the Plio-Pleistocene suids, although the later *Metridiochoerus compactus* had the most hypsodont molars (Harris and White 1979). The average body mass for *Notochoerus euilus* has been estimated to be 433 kg, and for *Notochoerus scotti* 542 kg (pers. comm. Juha Saarinen, based on the dimensions of the second molars, after Janis 1990b).

In the Turkana Basin database, all but three specimens of kolpochoeres are referred to as *Kolpochoerus heseloni*. The three has been referred to as *K. majus*. However, many species of kolpochoeres have been recognised throughout Africa (Brunet and White 2001, Haile-Selassie and Simpson 2013, Souron et al. 2013). Some specimens from the Turkana Basin localities from Pleistocene could be assigned to *K. olduvaiensis*, which is described to be a daughter taxon to *K. heseloni* with longer third molars (Gilbert 2008). The Turkana Basin kolpochoeres had third molars that increased in height and length during their evolutionary lineage (Cooke and Maglio 1972). However, they never became as hypsodont as *N. scotti* or *M. compactus* (Cooke 2007). Compared to *Notochoerus* and *Metridiochoerus* species, *Kolpochoerus* had thicker enamel bands (Fig. 4D). Isotope studies have demonstrated that *Kolpochoerus* was a dominant C4 consumer, which is not consistent with the evolution of its teeth, because the teeth did not become as hypsodont as some of the *Metridiochoerus* species or *Notochoerus scotti* (Harris and Cerling 2002, Cerling et al. 2015, Fig. 3). Post-cranial studies have indicated intermediate habitats for *Kolpochoerus heseloni* (Bishop 1999). The average body mass for *K. heseloni* has been estimated to be 297 kg (pers. comm.

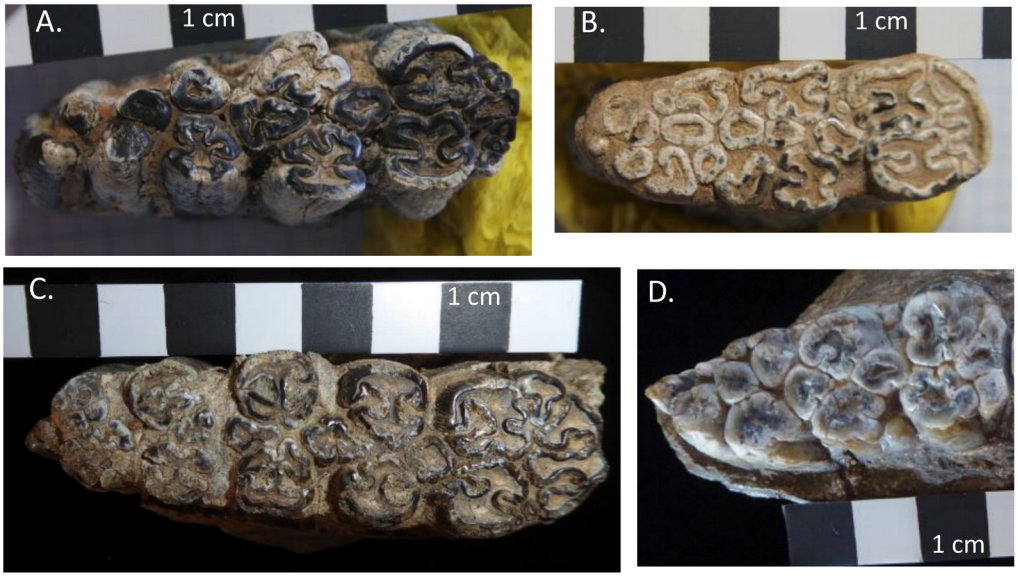

Figure 4. Examples of the upper third molars of the Plio-Pleistocene Turkana Basin suids. A. *Notochorus euilus*, B. *Metridiochoerus andrewsi*, C. *Notochoerus scotti* and D. *Kolpochoerus heseloni*.

Juha Saarinen, based on the dimensions of the second molars, after Janis 1990b).

Metridiochoerus appeared in the Turkana Basin in the Pliocene. The Turkana Basin database includes four species of *Metridiochoerus*: *M. andrewsi*, *M. hopwoodi*, *M. modestus* and *M. compactus*. Most of the *Metridiochoerus* species had hypsodont cheek teeth (Fig 4B), although the earliest (ca. 3.4 Ma) specimen found from the Usno Formation, Ethiopia, had a rather low crown height (White et al. 2006). Their crown height increased throughout the Pliocene and the Pleistocene, culminating in the late Pleistocene *Metridiochoerus compactus*, which possessed molars that could be over 20 cm in height (Harris and White 1979, Cooke 2005). Isotope studies have demonstrated that *Metridiochoerus* species consumed mostly C4 plants throughout their history (Fig. 3). The average body mass for *M. andrewsi* has been estimated to be 199 kg and for *M. compactus* 560 kg (pers. comm. Juha Saarinen, based on the dimensions of the second molars, after Janis 1990b). Pickford (2013) has estimated the body mass of the late *M. andrewsi* from South Africa based on tibio-talar joint dimensions to be 270-380 kg +/- 50 kg.

The much smaller *M. modestus*, which lived at the same time as *M. compactus*, has been considered to be the ancestor of *Phacochoerus* (Pickford 2012). The average body mass for *M. modestus* has been estimated to be 95 kg (pers. comm. Juha Saarinen, based on the dimensions of the second molars, after Janis 1990b).The major difference between the molars of *Metridiochoerus* and *Phacochoerus* is the enamel folding: *Metridiochoerus* has prominent folds in its enamel rings that make them h-shaped or y-shaped, whereas *Phacochoerus* has roundish enamel rings. In addition *Phacochoerus* is smaller than most of the *Metridiochoerus* species.

The shift to a higher crown and more cusp pairs in the third molars emerged independently in *Nyanzachoerus-Notochoerus*, *Kolpochoerus*, and *Metridiochoerus* in the Plio-Pleistocene eastern Africa. In the Turkana

Basin, *Notochoerus scotti* and *Metridiochoerus compactus* demonstrated extreme hypsodonty and horizodonty in their molars, while the changes in *Kolpochoerus heseloni* were less extreme.

1.5 Objectives of the thesis

The aim of this thesis is to study the circumstances of morphological dental changes of suids in several lineages in the Plio-Pleistocene eastern Africa by studying fundamentals of dental wear with a mechanical masticator and by analysing the dental adaptations of the suids as well as their dietary, environmental and evolutionary implications.

To reach the objective, this thesis addresses the following research questions:

1. Can we reproduce dental wear with a mechanical masticator and use it to analyse differences between diets?

Microwear analysis is a commonly used method for identifying diets (Walker et. 1978, Solounias et al. 1988, Teaford and Walker 1984, Hunter and Fortelius 1994, Merceron et al. 2004) but experimental testing of its reliability is rare. In this thesis I conducted research with a mechanical masticator to compare microwear generated by diets with different amounts and kinds of abrasive particles.

2. What causes the observed difference in dental wear between browse and graze diets?

Studies from living animals indicate that grazers often have more scratches in their microwear pattern, while browsers have more pits (Solounias et al. 1988, Solounias and Moelleken 1992, Mainland 2003). However, few studies clearly demonstrate that the microwear comes from the diet. In this thesis I used a mechanical masticator to test if similar results could be achieved in a simplified laboratory experiment with diets that contain different amounts of abrasives. In addition, I tested the overall wear of the different diets because it has rarely been studied experimentally.

3. How much does grit impact dental wear?

The wear produced by exogenous grit and dust in food items has been hypothesised to be part of the evolution of hypsodonty (Healy and Ludwig 1965, Damuth and Janis 2011). Increased quantities of open habitats and greater aridity may have impacted the evolution of the Turkana Basin suids by increasing grit and dust in their diets. In this thesis, I studied the impact of sand grains on enamel by adding sand grains to one diet in the mechanical masticator experiments.

4. Did the Plio-Pleistocene suids of the Turkana Basin differ in their habitats and respective dietary preferences as they rose and fell in abundance during their history?

In this thesis I studied the relative abundances of the Turkana Basin suids from locations dated between 8 Ma to 0.7 Ma. By demonstrating when the suid genera peaked and fell we can infer the ecological relation between the suid genera and the changes in climate and environment.

5. Can we classify the diets of extant suids from patterns of their dental topography?

All suids are omnivorous, though some prefer certain types of foods (Meijaard and Melletti 2017). For example warthogs generally consume grasses, but they can also dig

roots and eat from carcasses. In this thesis I studied the dental topography, measured by mean surface slope, relief index, angularity, sharpness index, Dirichlet normal energy and orientation patch count analysis, of the grazing warthog (*Phacochoerus* spp.), the mixed-feeding forest hog (*Hylochoerus meinertzhageni*), the omnivorous tropical forest suids the bushpig (*Potamochoerus* spp.) and the babirusa (*Babyrousa* spp.), and the omnivorous generalist wild boar (*Sus scrofa*). I aimed to identify the relationship between dental topography and diet preferences.

6. What was the diet of the Plio-Pleistocene Turkana Basin suids compared to the extant suids?

Isotope analyses and morphological adaptations of the Turkana Basin suids have suggested that they gradually adapted more and more towards grazing lifestyle (Harris and Cerling 2002, Cerling et al. 2015). In this thesis, I studied the adaptation for grazing by comparing the dental topography of fossil suids (*Notochoerus euilus*, *Notochoerus scotti*, *Kolpochoerus heseloni* and *Metridiochoerus andrewsi*) to present-day suids, which include omnivorous, mixed-feeding and grazing species. The hypothesis was that if the fossil suids of the Turkana Basin were grazers, they would have similar dental topography to the extant grazing warthog.

2 Study region

The data used in paper II and the fossil suid specimens in paper III come from the Turkana Basin (Fig. 5). The Turkana Basin Paleontology Database (https://naturalhistory.si.edu/ete/ETE_Datasets_Turkana.html) is freely available from the National Museums of Kenya. The database comprises fossil mammal specimens found in the Kenyan part of the Turkana Basin.

2.1 The Turkana Basin

The Turkana Basin, or Omo-Turkana Basin, is situated in northern Kenya and southern Ethiopia in the East African Rift. Nowdays the Lake Turkana is situated in the middle of the basin. Most of the lake is situated in Kenya, but the basin is part of the lower Omo Valley of Ethiopia. The River Omo provides most of the water input of the Lake Turkana: the water flows from the Ethiopian highlands through the lower Omo Valley to the Lake Turkana (Yuretich and Cerling 1973). The present day basin origins from the Pliocene tectonic developments of the modern rift system and the history of the alkaline Lake Turkana goes back more than 200 000 years (Yuretich and Cerling 1973, Feibel 2011). Due to millions of years of fluvial activity in the basin, sedimentation has been continuous (Feibel 2011). The sediment layers contain a rich fossil record from the Miocene to the Pleistocene. The dating of the layers has been possible due to the presence of volcanic ash (otherwise known as ‘tuff’) layers between members (Brown and McDougall 2011). The tuff layers can be dated by radiometric methods (McDougall and Feibel 1999). Furthermore, the tuff layers can be identified in different parts of the basin by their individual mineral composition, even

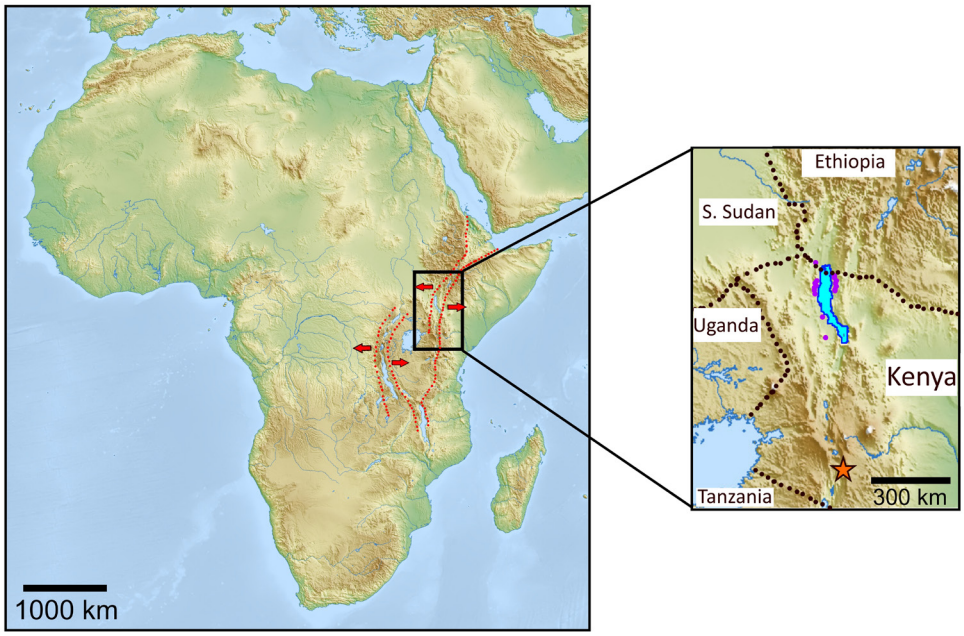

Figure 5. The Turkana Basin is situated in northern Kenya. In the left side image red lines indicate rift margins and arrows the directions of the rifting. Lake Turkana (highlighted in the right side image) is located in the middle of the Turkana Basin. Fossil localities are depicted in purple dots around the Lake Turkana. Nairobi is indicated by the orange star. Edited from mapswire.com (CC-BY 4.0).

though they are not continuous (Cerling et al. 1979, WoldeGabriel et al. 2005, Brown and McDougall 2011).

In addition to a vast animal fossil record, several important hominids have been found in the Turkana Basin, including the famous "Turkana Boy", a nearly complete skeleton of a young *Homo erectus* (Brown et al. 1985). Furthermore, other significant finds like *Australopithecus anamensis* (Leakey et al. 1998) and *Kenyanthropus platyops* (Leakey et al. 2001) have been discovered in the basin that has been nicknamed 'the Cradle of Humankind'.

The present-day Turkana Basin is hot and dry: mean annual precipitation is approximately 200 mm, and mean annual temperature is around 30°C (Ogallo 1981, Nicholson 2000, weatherbase.com). In the Köppen-Keiger climate classification, the Turkana Basin is classified as an arid and hot desert (BWh) (Peel et al. 2007). There are few large wild animals in the area (Watson 1969). Warthogs are the only suids that can be encountered in the southern parts of the Turkana Basin today (Watson 1969).

2.2 Shifting environmental conditions in eastern Africa from the late Miocene to Pleistocene

The deep sea oxygen isotope record show a global cooling trend from the early Miocene to the Pleistocene (Zachos et al. 2001). The cooling trend and the subsequent aridity have been used as an explanation for major faunal and floral changes during the last 10 Myr.

Changes in Earth's orbital precession, obliquity, and eccentricity affect climate in 23-19-kyr, 41-kyr and 100-kyr cycles respectively (deMenocal 1995). The wet and dry conditions before 2.8 Ma were apparently regulated by orbital precession changes (deMenocal 1995,

2004). As high latitude ice sheets were growing 41-kyr cycles dominated during 2.8-1.2 Ma and then the climate shifted to 100-kyr glacial cycles after 1.2-0.8 Ma (deMenocal 2004). It is still debated if these Milankovitch cycles were responsible for some faunal turnovers (Barnosky 2001, Faith and Behrensmeyer 2013).

Stable carbon isotope measurements and palaeoprecipitation calculations from palaeosols have indicated increased C4 biomass and aridification in the Turkana Basin during the last 4.3 Myr (Wynn 2004). However, the oxygen isotope record has demonstrated that there was no long-term aridification in the Plio-Pleistocene Omo-Turkana Basin (Blumenthal et al. 2017). However, there were variable climate conditions with increased aridity punctuations around 3.58-3.35 Ma, 2.52-2 Ma and 1.81-1.58 Ma (Wynn 2004). Between 1.9-1.7 Ma a large freshwater lake was situated in the Turkana Basin (Trauth et al. 2005). Furthermore, palaeosols have been used to estimate the woody cover in the Turkana Basin area during the late Miocene to Pleistocene. The study of Cerling et al. (2011) demonstrated that the Turkana Basin's landscape was relatively open in the late Miocene and followed by an increase in the woody cover in the middle Pliocene. Open environments returned by 1.8 Ma, and the time afterwards was a culmination of the long-term trend of shrinking woodlands (Cerling et al. 2011).

The fauna of the Omo sequence from southern Ethiopia has indicated that closed woodland and forest taxa declined from 3.6 Ma to 2.1 Ma, and woody grassland taxa increased at the same time, surpassing the closed woodland taxa around 2.4 Ma (Bobe et al. 2002). Analysis of the Turkana Basin's mammal data has indicated that woodland taxa persisted from 3 to 2 Ma, although new grassland species also appeared, which indicates the heterogeneity of the habitats (Behrensmeyer et al. 1997). Bovids have been used to interpret palaeoenvironments and changes from closed to open habitats in eastern Africa. Bovids are an abundant group and include genera that favour both environments. The bovid record has suggested that the environment was highly variable through the Plio-Pleistocene in the Omo-Turkana Basin (Kappelmann et al. 1997, Plummer et al. 2015, Negash et al. 2015, Barr 2015). In addition, abundances of open adapted bovids (Alcelaphini, Antilopini and Hippotragini) have suggested an increase in open and seasonally arid grasslands of about 6.5 Ma, 3 Ma, and 1.6 Ma in the Turkana Basin (Bobe 2006).

3 Materials and methods

3.1 Mechanical masticator and microwear analysis

In paper I, a mechanical masticator (Fig. 6) built in the University of Helsinki, according to our specifications for the chewing experiments, was used. The machine can hold one tooth pair. One tooth is attached to a moving arm, which makes a back-and-forth movement. The other tooth is attached to a flexible stationary arm, so that when the moving tooth hits the stationary tooth, it yields slightly, making the teeth's contact sliding rather than smashing. The contact of the teeth occurs when the moving tooth moves towards the stationary tooth. Thus, the movement during the contact of the teeth is unidirectional.

Horse cheek teeth were used in the experiment as a model teeth because they are relatively large, and feature enamel, dentine and cementum on their surface. The chewing results were expected to apply for example for

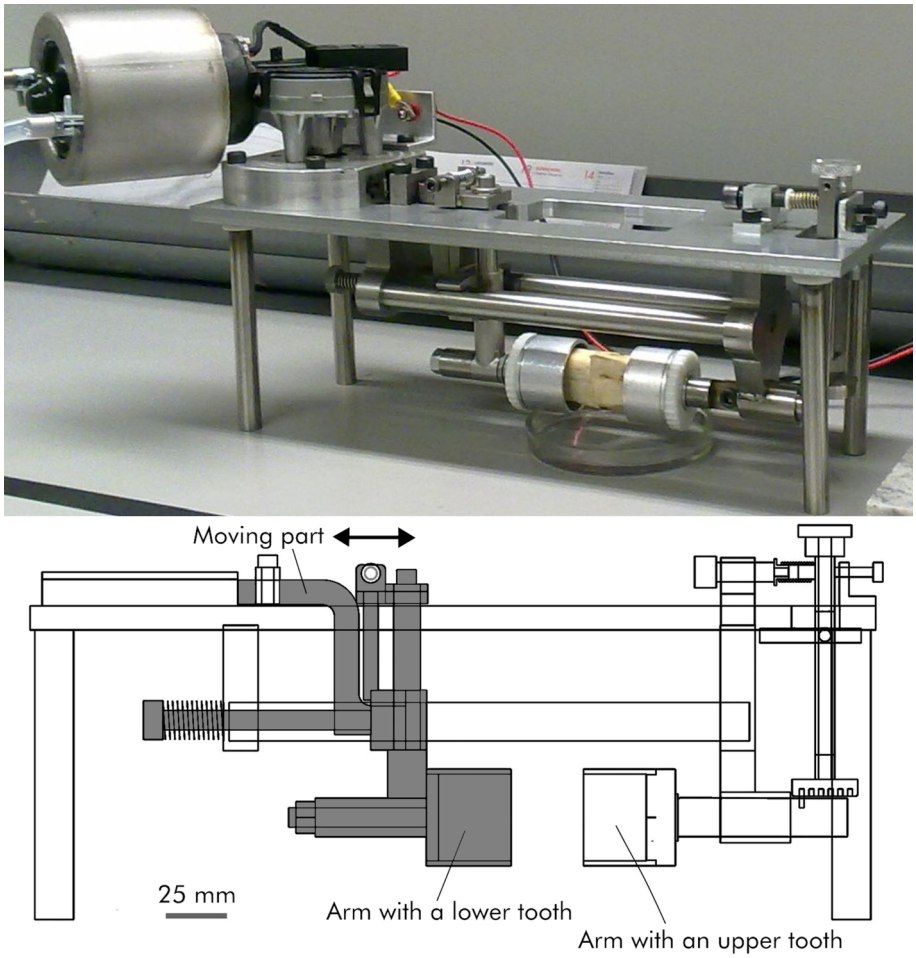

Figure 6. Chewing machine. Photo by J. Rannikko, sketch by Aleksis Karme.

suids because enamel, dentine and cementum are visible on the surface and the chewing movement is simplified.

The roots were cut off and the teeth were glued with epoxy into plastic rings, which could be attached to the chewing machine. The occlusal surface of the teeth was cut and polished. After polishing, the teeth were attached to the machine and submerged in the food material during the operation. Four different food materials were used, and their abrasiveness was measured as the amount of acid detergent insoluble ash in dry matter (g/kg): lucerne (5 g/kg), grass (16 g/kg), grass with rice hulls (24 g/kg) and grass with rice hulls and sand (77 g/kg). In addition five pairs of teeth chewed in water only to simulate wear by attrition.

Silicone moulds and epoxy casts were made from the occlusal surface after 6 hours and 30 minutes of chewing. Microwear was studied from the enamel bands of the teeth from images taken from the casts. The images of the enamel bands were taken with a light microscope with 32x magnification.

A light microscope was used instead of a scanning electron microscope (SEM) because of easier access and affordability.

Light microscopes have been successfully used in other microwear studies (Solounias and Semprebon 2002, Merceron et al. 2004, Merceron et al. 2005, Rivals et al. 2014). However, the results cannot be compared with SEM results because of the different manification.

Microware 4.02 (P. Ungar, Fayatteville, Arkansas, USA) was used to identify small (length less than 20 mm), large (length 20–50 μm) and very large (length more than 50 μm) pits as well as thin (width less than 15 μm) and wide (width more than 15 μm) scratches from an area of 0.4 mm x 0.4 mm inside the central enamel band (Merceron et al. 2005, Merceron et al. 2012).

The overwriting potential of the diet was estimated by polishing the tooth surface with a 68 μm sanding machine before chewing and calculating the amount of polishing striation left after the chewing. Teeth were positioned in the mechanical masticator so that scratches due to chewing (parallel to chewing direction) could be differentiated from the initial polishing striation (perpendicular to the chewing direction). Furthermore, a tooth pair from each diet group was computed tomography (CT)-scanned before and after the chewing. The overall wear was calculated from the CT-scans.

3.2 Relative abundance

Paper II examined the relative abundance of the suid genera in the Turkana Basin between the late Miocene and early Pleistocene. Relative abundance refers to the percent of a certain group of individuals relative to the total number of the individuals in the area.

Different fossil localities yield different amounts of fossil specimens. Thus, relative abundance is a convenient proxy to analyse abundances as it is robust to variation in sample size.

Palaeoecological studies have often used occupancy as an equivalent for abundance (Jernvall and Fortelius 2004, Foote et al. 2007, Fortelius et al 2014). Occupancy does not count how many individuals of a specific species or genus are in a locality. Instead, occupancy measures how many localities the species or genus is found in during a time interval, relative to the localities known from that period and area.

The data in paper II came from an updated version of the Turkana Basin Database, which has been complemented by other datasets for Lothagam, Kanapoi and localities on the western side of the Lake Turkana (curated by Meave Leakey) (Fortelius et al. 2016). The data (i.e. specimens that have information about their age and genus) included 8,489 individual mammal specimens of which 1,784 were suids. The relative abundances of the suid genera among all mammal genera were calculated by dividing the number of specimens from one genus by the amount of all the specimens found from specific members. The results are presented as percentages. Relative abundances were used instead of absolute numbers because some localities, and thus members, are more intensively sampled or yield more specimens than others. The analysis was done in the genus level (except with *N. euilus* and *N. scotti*), because misidentifications become more likely past that point; also, due to the gradual changes in the morphology there are still some disagreements about the number of species present.

Suids have been frequently collected for biostratigraphy and taxonomy studies (Cooke and Maglio 1972, Harris and White 1979). This, combined with the easy identification of suid teeth, has undoubtedly led to the extensive

collection of suid specimens, which has an effect on the relative abundance of suids among other mammals in the collections. The relative abundances of fossil taxa most likely do not necessarily reflect the abundances of species in the living communities; suids as a group are most likely overrepresented. Within the suid family, however, the relative abundances of suid taxa are nevertheless likely to reveal the differences between the individual suid genera over time.

3.3 Dental topography analyses

Paper III used dental topography analyses for the third molars of fossil and extant suids. The use of geographic information system (GIS) tools for dental topographic analysis and their relation to diet started twenty years ago (Reed 1998, Zucotti et al. 1998, Hunter and Jernvall 1998, Ungar and Williamson 2000). This method seeks to analyse tooth surfaces as 3D landscapes (Zucotti et al. 1998, Ungar and Williamson 2000). The use of a GIS approach to study dental topography enables the taking of measurements from the whole occlusal surface and is independent of landmarks, unlike in geometric morphometrics (Ungar and Williamson 2000, Evans 2013). Paper III analyses the relief index (RFI), mean surface slope (MSS), angularity, sharpness index (SHI), Dirichlet normal energy (DNE) and orientation patch count (OPC).

The ratio of the 3D surface of a tooth to its projected 2D surface is called a relief index. This relief index reflects the occlusal relief; the higher the RFI, the higher the occlusal relief (M'Kirera and Ungar 2003, Ungar and Williams 2000). Diets of different primate species have been differentiated with the RFI. Species that eat more leaves have higher RFI than frugivores (Boyer 2008, Boyer et al. 2010).

The mean surface slope from the whole 3D surface represents the steepness of the cusps (Ungar and M'Kirera 2003). The MSS usually decreases when the tooth wears down (Ungar et al. 2018).

Angularity is the second derivative of elevation (otherwise known as the slope of the slope) (Ungar et al. 2018). Angularity measures surface jaggedness: as Ungar and M´Kirera (2003) described, the difference between slope and angularity is 'analogous to the difference between the sharpness of a knife and its serratedness'.

The proportion of steeply sloped parts of the surface is called sharpness in Karme 2008, Karme et al. 2010, and Ungar et al. 2018. Due to the fact that sharpness typically means cutting ability of an edge, I refer it as sharpness index (SHI) in this thesis. SHI is determined by the natural breaks method classification. The natural breaks method divides the surface slopes into three categories, which have variation that is as small as possible within the groups and is high as possible between the groups. Then, the relative proportion of each category is calculated on the tooth surface. The relative proportion of the highest slope category is the SHI (Karme 2008).

Dirichler normal energy is independent of manual orientation and scale (Bunn et al. 2011, Winchester 2016). Dirichlet normal energy measures the deviation of a surface from being planar (bending of the surface) (Bunn et al. 2011). In paper III it was discovered that DNE analysis is highly sensitive to artefactual errors in 3D meshes and how the meshes are pre-processed.

Most of the dental topography studies that utilize GIS tools have focused on primate teeth and diets (M'Kirera and Ungar 2003, Ungar and M'Kirera 2003, Dennis et al. 2004, Boyer 2008, Bunn and Ungar 2009, Winchester et al.

2014, Pampush et al. 2016, Yamashita et al. 2016, Ungar et al. 2018), though at least one has included rodents with primates (Prufrock et al. 2016). However, OPC analysis, which is based on geographical orientation of patches on the tooth surface, has been used for other animal groups (Evans et al. 2007, Evans and Jernvall 2009, Santana et al. 2011, Smits and Evans 2012, Wilson et al. 2012, Evans and Janis 2014). Orientation patch count measures the complexity or heterogeneity of the tooth surface. It was first used to separate the trophic levels in two independent evolutionary lineages, carnivorans and rodents (Evans et al. 2007). Afterwards, an upgraded version, orientation patch count rotated, was demonstrated to separate browsing and grazing in horses (Evans and Janis 2014).

In paper III, dental topography analyses were applied extensively to suids for the first time. Mean surface slope and sharpness index have been analysed for a few suid second molars in Karme 2008. The aim in paper III was to identify a relationship between the diet and dental topography in the present-day suids with a number of dental topography techniques. Furthermore, the dietary preferences of the Plio-Pleistocene Turkana Basin suids and the Miocene listriodontines from Eurasia were studied in relation to the extant suids. The extant suid specimens were scanned in the Natural History Museum of Berlin, Germany. The Turkana Basin suid specimens were scanned from the collections of the National Museums of Kenya. The Miocene specimens were scanned from the cast collection of M. Fortelius in the University of Helsinki. The original Miocene specimens are housed in the University of Ankara, the Natural History Museum of Basel, the Natural History Museum London, the National Museum of Zurich and the University of Utrecht.

4 Overview of the original publications

4.1 Paper I: Mechanical modelling of tooth wear (Karme and Rannikko et al. 2016)

The role of extrinsic grit and internal minerogenic plant parts (phytoliths) in tooth wear has been debated for decades (Baker et al. 1959, Healy and Ludwig 1965, Sanson et al. 2007, Lucas et al. 2014, Xia et al. 2015). The aim of this study was to conduct laboratory-condition tests on how food items with different amounts of abrasive particles wear teeth and generate microwear on enamel. A mechanical masticator was used in the experiment. Four diets (lucerne, grass, grass-rice, and grass-rice-sand) were chewed with horse teeth. Lucerne was equivalent to the browse diet in the experiment. Microwear of the enamel was observed with a light microscope, and pits and scratches were calculated from the surface images with the Microware 4.02 program (P. Ungar, Fayetteville, Arkansas, USA). The total wear of the teeth was calculated from the difference of the CT-scans before and after the chewing procedure.

The microwear signal was strikingly similar in all non-sandy diets. This contradicted the hypothesis that lucerne, which contains lower amounts of phytoliths, would be more pit-dominated than grass and grass-rice diets. This could be due to our laboratory setup with simplified back-and-forth chewing procedure. However, the overall wear rate of the lucerne diet was slower than the wear rates of other diets. The grass-rice-sand diet had more very large pits and less thin scratches than the non-sandy diets. The amount of wear was from highest to lowest: grass-rice-sand (0.134 mm), grass-rice (0.067 mm), grass (0.060 mm), attrition (0.008 mm), and lucerne (0.003 mm).

All diets used, as well as attrition, generated microwear markings on the tooth enamel. In the laboratory setup used in this study, the microwear was very similar between diets, which varied in their abrasive content. However, added sand grains heavily damaged the tooth surface, including the enamel.

The results demonstrated that the grass-based diets had a higher overall wear rate, although the microwear signal was not significantly different. This is evidence that the internal characteristics of the grass was more abrasive than those of the lucerne.

4.2 Paper II: Relative abundances and palaeoecology of four suid genera in the Turkana Basin, Kenya, during the late Miocene to Pleistocene (Rannikko et al. 2017)

Paper II focused on the changes in relative abundance between the suid genera of the Turkana Basin from the late Miocene to early Pleistocene. During the Plio-Pleistocene, suids in Africa developed dental traits that are associated with a grazing diet: long and hypsodont molars, cement cover and complicated enamel crenulation (Harris and White 1979). Similar adaptations among suids have been recorded only in the *Hippohyus* and *Sivahyus* that were found in the late Miocene of the Indian subcontinent (Pilgrim 1926). The aim of the study was to understand how a C4-diet specialist group reacted to environmental changes during the Plio-Pleistocene in the Turkana Basin in environments that also were home to the early hominins.

The relative abundances of four suid genera from 8 to 0.7 Ma, namely *Nyanzachoerus*, *Notochoerus*, *Kolpochoerus* and *Metridiochoerus*, were calculated from a large dataset of the Turkana Basin mammals. The relative abundances of the suid genera among all mammal genera were calculated by dividing the number of specimens from one suid genus by the amount of all the mammal specimens found from specific geological members.

The results indicated that all genera peaked in different time intervals. The highest relative abundance of *Nyanzachoerus* was at the start of our time intervals in the late Miocene. After the first time interval, *Nyanzachoerus* declined steadily, and was not found in locations that are younger than 2 Myr. *Notochoerus* peaked in 3.44-2.53 Ma, and the decline of *Notochoerus* occurred at the same time as an increase in *Kolpochoerus* abundance 2.53-1.87 Ma. The domination of *Metridiochoerus* started after 1.87-1.48 Ma, while *Kolpochoerus* was still abundant.

The compilation of $\delta^{13}C$- and $\delta^{18}O$-values from the literature indicated that *Notochoerus* shifted to more positive $\delta^{13}C$-values, but *Metridiochoerus* and *Kolpochoerus* stayed at similar values (Harris and Cerling 2002, Cerling et al. 2015). *Kolpochoerus* had the lowest $\delta^{18}O$-values, which might indicate dependence on a regular water source. *Metridiochoerus* was divided into two groups of lower and higher $\delta^{18}O$-values (Harris and Cerling 2002).

Reduced tree cover and expanded grasslands might have been the reason for the disappearance of the *Nyanzachoerus* species and their evolution to the *Notochoerus* species. Nyanzachoeres might have been inhabiting denser vegetation and riparian woodlands, much like the extant *Potamochoerus porcus* (Kingdon 1979), but tree cover was greatly reduced over eastern Africa around 6.3 Ma (Cerling et al. 2011). Adaptations in *Notochoerus* were possibly enhanced by the cooling and drying in the African climate in the late Pliocene (Liddy et al., 2016; deMenocal, 1995).

Kolpochoerus and *Metridiochoerus* were both abundant from 1.87 Ma until the late Pleistocene. They probably had different ecological niches: *Kolpochoerus* stayed in the more wooded areas while *Metridiochoerus* was adapted to open grasslands.

4.3 Paper III: The case of the grazing suids in the Plio-Pleistocene Turkana Basin: 3D dental topography in relation to diet in extant and fossil pigs (Rannikko et al. in review)

Paper III studied the dental surface topography of extant and fossil suid species. The study had two objectives: 1) to quantify the relationship between dental topography and diet (omnivorous, grazing, and mixed-feeding) of present-day suids and 2) to apply the results from the extant species to the Turkana Basin suids to test the current interpretation that the Plio-Pleistocene suids were adapting to a grazing diet. In addition, we included Miocene *Listriodon* spp. as a model for the browsing suid.

The hypothesis was that the dental topography of the third molars of the Plio-Pleistocene suids differed significantly from all other extant suids (and *Listriodon*) except for the warthog (*Phacochoerus*), which is the only living suid that displays dominant albeit selective grazing behaviour.

Three-dimensional scans were obtained from (upper/lower) third molars of the extant suids *Phacochoerus africanus* (15/15), *Potamochoerus* spp. (15/15), *Hylochoerus meinertzhageni* (4/4), *Sus scrofa* (15/15) and *Babyrousa* spp. (5/5). Fossil specimens of the Turkana suids included (upper/lower) *Notochoerus euilus* (6/0), *Notochoerus scotti* (3/1), *Kolpochoerus heseloni* (6/1) and *Metridiochoerus andrewsi* (5/4). Miocene suids included *Listriodon* spp. (6/7). Every specimen was analysed for mean surface slope (MSS), angularity, sharpness index (SHI), relief index (RFI), Dirichlet normal energy (DNE) and orientation patch count (OPC). The DNE analysis of the Turkana Basin fossil specimens produced high values and large variation, which could be due to the preservation of the fossil specimens and artefactual scanning errors due to the size and complexity of their teeth.

The grazing *Phacochoerus* had low MSS, high OPC, low RFI, low SHI, and high angularity. The mixed-feeding *Hylochoerus* had high MSS, low OPC, high RFI, high SHI, and medium angularity. The present-day omnivorous suids had MSS, RFI and SHI between that of the two herbivorous suids. *Potamochoerus* and *Babyrousa*, the most frugivorous suids, had low OPC and low angularity, while *Sus* had medium angularity and OPC. *Phacochoerus*, the only dedicated grazer among the extant suids, differed significantly from the other extant suids in all the analyses except DNE. The mixed-feeder *Hylochoerus* could be separated from the omnivorous suids by its results on MSS, RFI, and SHI. Finally, the tropical forest suids that prefer fruits and tubers, *Potamochoerus* and *Babyrousa*, could be separated from the generalist *Sus* by their lower OPC.

The browsing *Listriodon* had high MSS, SHI, and RFI like *Hylochoerus*, but its OPC and angularity were lower.

Notochoerus scotti and *Metridiochoerus andrewsi* were similar to *Phacochoerus* in terms of their OPC, angularity, SHI, and MSS. However, *Notochoerus euilus* and *Kolpochoerus heseloni* resembled *Phacochoerus* only in terms of their OPC and angularity, placing them between the present day omnivorous suids and the grazing suids.

The results demonstrate that *N. scotti* and *M. andrewsi* were most probably open area grazers, whereas *N. euilus* and *K. heseloni* were also grazers, although possibly in more closed environments where browse and underground storage organs were available.

5 Discussion

5.1 The importance of experimental research and multiproxy approaches (papers I and III)

Studying dental wear can help to understand long term trends of environmental change. Tooth wear is a long and complex process, and we often see only snapshots of the process when we examine the teeth of long dead animals. Some experiments have been conducted with living animals to study dental wear (Schulz et al. 2013, Müller et al. 2014). Recently, dental wear has been increasingly studied via laboratory experiments (Lucas et al. 2013, Xia et al. 2015, Hua et al. 2015). All experimental research is helpful for deciphering dental wear processes, and thus the lack of studies where the chewing process is combined with laboratory machinery is unfortunate. Paper I introduced the first mechanical masticator to use real teeth in a simplified chewing procedure. The results showed that microwear analysis alone did not classify the different diets significantly. During the experiment, all the diets generated a high number of scratches on the enamel. Only chewing in water, which did not include any food items, produced pit-dominated microwear pattern. The results represent a specific experiment procedure, which is a simplified simulation of the chewing process and does not take account unique habits of animals or chewing patterns for example. This simplified process might generate scratches more easily than pits.

The overall wear of the teeth was different between the diets. Thus, the turnover rate of microwear patterns differed between diets. The microwear marks accumulate on the surface and overlap when the wear is higher. Although the chewing machine was not a precise analogy of chewing in a live animal, it can be assumed that the same principles of accumulating microwear marks and the turnover of the patterns would likely apply to real chewing and dental wear.

The chewing machine experiment demonstrated that one proxy might not be able to distinguish different diets. A multiproxy approach for African Plio-Pleistocene suids has been used in Bishop et al. (2006). The researchers used dental microwear analysis, isotope analysis and ecomorphological analysis of limb bones to assess palaeoecology and its change through time for a single species, *Kolpochoerus heseloni*. Microwear analysis, isotope analysis and limb bone analysis have been conducted from other Plio-Pleistocene African suids in separate studies (Bishop 1999, Harris and Cerling 2002). In paper III, another viewpoint was added to the palaeoecology studies of the Plio-Pleistocene African suids: the dental surface topography of fossil and extant suids was analysed. Dental surface topography analyses have been used mainly for primates and only for a few other animal groups (M'Kirera and Ungar 2003, Ungar and M'Kirera 2003, Dennis et al. 2004, Boyer 2008, Bunn and Ungar 2009, Winchester et al. 2014, Pampush et al. 2016, Prufost 2016, Yamashita et al. 2016, Ungar et al. 2018). Paper III applied dental topography analyses to suids in this extend for the first time. The results support the earlier findings that *N. scotti* and *M. andrewsi* were grazers and *N. euilus* and *K. heseloni* inhabited intermediate

habitats (Bishop 1999, Bishop et al. 2006). The results of my research complement the palaeoecological interpretations of the Plio-Pleistocene suids of the Turkana Basin.

5.2 Palaeoecology of the Plio-Pleistocene Turkana Basin suids (papers II and III)

It is not certain why the evolution towards grazing in suids occurred in many lineages in Africa and not so much elsewhere. It is also not certain why the dietary shift occurred from the early Pliocene onwards when the spread of grasslands started already in the Miocene. However, two suids in northern India, *Hippohyus*, and its smaller relative *Sivahyus*, did develop hypsodont teeth with highly folded enamel in the late Miocene and early Pliocene (Pilgrim 1926, Colbert 1935). Therefore *Hippohyus* and *Sivahuys* evolved hypsodont and complex enamel folding at least one million years before *N. scotti* and three million years before *M. compactus*. In contrast to the Turkana Basin suids, *Hippohyus* and *Sivahuys* were smaller in size.

This raises the questions of what the drivers of those adaptations were in the late Miocene India and whether those drivers were the same as in the middle Pliocene in eastern Africa. Evidence of open C4 grasslands dating back to 7 Myr have been found in northern Pakistan (Barry et al. 2002). In Africa, C4 grasses rose to ecological dominance from 8 Ma to 3 Ma (Edwards et al. 2010), and open landscapes dominated by C4 biomass emerged only in the early Pleistocene (Ségalen et al. 2007). The later opening of vast grasslands could explain why the Turkana Basin suids adapted to grazing much later than the suids from northern India. Thus, the same factor, namely the spreading of the grasslands, might have been driving the adaptations in both areas. However, from the results of this thesis it is not possible to answer of what extend the Plio-Pleistocene suids in the Turkana Basin adapted to grazing in itself or to possible cycle of seasons or harsh time periods.

In paper I it was calculated that a 12 cm horse tooth would last for around 30 years with a grass diet, which is a good age for a domesticated horse. With the diet including sand grains, the tooth would last around 13 years, roughly a lifespan of a wild zebra. In contrast, with a lucerne diet the tooth would last over 600 years. These results point out the interesting connection between the duration of teeth and the life history of an animal (Skogland 1988), including maximum age of an individual. When teeth are worn out it is fairly impossible for a wild animal to survive as teeth are its only tools for process food. Animals that have hypsodont teeth can process abrasive food items longer time periods or repeatedly for example during harsher seasons. Neither *Notochoerus* nor *Kolpochoerus* species achieved the same level of hypsodonty than the late *Metridiochoerus compactus*, even though they added extra cusp pairs to their third molars. That could be a signal that *Notochoerus* and *Kolpochoerus* species developed hypsodonty for coping possible fall back to grasses, while *Metridiochoerus* truly adapted to mainly consume grasses and thus needed all the extra crown for maintaining its lifespan.

The shift from omnivory to grazing seems unlikely, as omnivores are usually more generalist and able to survive on a variety of foods in a less consistent environment. Suids were hardly the first ones to take advantage of the spreading grasslands. By the Miocene, other mammals in the Turkana Basin had already started to show adaptations to grazing (Bobe 2006, Cerling et al. 2015). Isotope studies and molar morphology have demonstrated that the shift to C4 diets in the eastern African suids

started around 5 Ma, but the hypsodont forms of suids emerged only after 3.5 Ma (Cerling et al. 2015).

Almost all present-day suids are omnivorous in a sense that they can consume herbaceous foods, insects and other animal products. But for example *Phacochoerus* mainly consumes grasses (Ewer 1958). The results in the paper III indicated that the grazing *Phacochoerus* had a different dental topography, measured by MSS, RFI, angularity, SHI and OPC, from omnivorous suids (*Potamochoerus, Sus* and *Babyrousa*) and *Hylochoerus*, which mainly consumes herbaceous foods, but is a mixed-feeder between browsing and grazing. Thus, the dental topography analyses can identify a relationship between diet and tooth morphology in the extant suids.

In terms of the dental topography, *Notochoerus scotti* and *Metridiochoerus andrewsi* resembled *Phacochoerus*, whereas *N. euilus* and *K. heseloni* indicated similarities with both the omnivorous suids and *Phacochoerus*. *Metridiochoerus andrewsi* is closely related to *Phacochoerus* (Cooke 1978, Kullmer 1999), which could explain the similarities, but *N. scotti* evolved similar molars independently.

It is likely that the extinct suids of the Turkana Basin were also omnivorous, but grasslands might have been a high-quality resource (Paine et al. 2018) that the suids could have been exploited. *Notochoerus scotti* and *Metridiochoerus andrewsi* were presumably dominantly grazers in open grasslands. Both *N. euilus* and *K. heseloni* have been assumed to live in closed or intermediate environments (Bishop 1999), and their diets were probably similar (paper III). In paper II *N. euilus* was demonstrated to disappear right before *K. heseloni* started to be abundant, which indicates either that *K. heseloni* replaced *N. euilus* by having an advantage in the environment, or the disappearance of *N. euilus* due to other reasons gave *K. heseloni* an opportunity to spread in the forest and woodland habitats of the Turkana Basin.

Both grasslands and forest environments have been part of the Turkana Basin since the late Miocene (Cerling et al. 2011). The wooded areas have been restricted to near the lake and rivers. Thus, during more arid times the wooded areas probably decreased along with the water bodies. Species that can exploit open grasslands persist during the decrease of wooded habitats. Therefore, adaptations towards abrasive foods started to emerge among nyanzachoeres and eventually lead to notochoeres. The relatively open conditions of the late Miocene and early Pliocene were followed by an increase in woody cover that peaked at around 3.6 Ma (Cerling et al. 2011), which is the same time as *Kolpochoerus* and *Metridiochoerus* appeared (paper II). Joordens et al. (2019) have suggested that hominins could have used forest corridors to reach inland basins in eastern Africa. Similarly, forest corridors could have been used by the early *Kolpochoerus* and *Metridiochoerus* which migrated from Eurasia as species that still favoured the wooded habitats (Kingdon 2003, Bobe 2006). Around 3 Ma, the hypsodont *N. euilus* was the most abundant suid in the Turkana Basin. *Notochoerus scotti* had appeared and nyanzachoeres were rare (paper II). The riparine forest niche was possibly open to the immigrants if *N. euilus* and *N. scotti* were inhabiting the wooded grasslands and arid shrublands. The final disappearance of *N. euilus* may have helped *K. heseloni* to become more abundant if they fitted in the same ecological niche. After kolpochoeres and metridiochoeres arrived in the inland basins as omnivorous species, they adapted to consume abrasive

foods in the same way as nyanzachoeres and notochoeres had done a million years earlier. *Notochoerus scotti* disappeared, which may have been because metridiochoeres were better at utilising the expanding open grasslands. *Metridiochoerus compactus* appeared after *N. scotti* had disappeared. Thus, they did not compete for the niche of the large grazing suid. The relative abundance results in paper II suggest that both *Kolpochoerus* and *Metridiochoerus* were abundant during the last 2 million years, which indicates that they had different ecological niches. Isotope analyses have indicated that both were consuming C4 plants (Harris and Cerling 2002, Cerling et al. 2015). Therefore they presumably inhabited different environments. *Kolpochoerus* probably inhabited the riparine forests (Bishop et al. 2006) while *Metridiochoerus* was adapted to the open savanna.

Warthogs do not ruminate. However, they have digestion adaptations that allow effective use of grass as a source of energy (Clauss et al. 2008b). They also select the fresh parts of the grass (Ewer 1958). The same abilities might have been the key element for *Metridiochoerus* to outcompete *Notochoerus* in the savanna. However, the extant *Phacochoerus* is smaller in size than *N. scotti* and *M. compactus*. They might have been too large to be selective feeders like *Phacochoerus* and thus relied on bulk feeding.

Kolpochoerus did not have to compete for grass consumption with *Metridiochoerus* if it mostly stayed in the riparine forest (Bishop et al. 2006). Although grasses are also part of the riparine environment, they might not be as abrasive as in arid open areas (Wilson et al. 1976, McNaughton et al. 1985) and their roots might be easier to dig in moist soil. Open grasslands also have more dust accumulation. Less abrasive foods and less dust would explain why *Kolpochoerus* did not acquire the same hypsodont and horizodont molars as *Notochoerus* and *Metridiochoerus* but still had the isotopic signal of a grazer (Harris and Cerling 2002).

5.3 Tooth wear in relation to the grazing diet, aridity, and the open landscape (papers I and III)

Grasses are demanding on chewing since they contain abrasive silica as opaline phytoliths and have thick cell walls that mainly consist of slowly digestible fibres (Twiss et al. 1969, Demmet and Van Soest 1985, Strömberg 2002). However, they are abundant, appear almost everywhere year round, and grow fast. Today, open habitats are widely distributed. Increasing hypsodonty has long been thought to be a sign of grazing and thus of the spreading of the grasslands (Stebbins 1981), because the grass diet wears teeth fast (paper I). Higher silica content increases the abrasiveness of grasses (Massey et al. 2006), but the effect on enamel is debated (Sanson et al. 2007, Damuth and Janis 2011, Rabenold and Pearson 2011, Lucas et al. 2013, Lucas et al. 2014, Xia et al. 2015). McNaughton et al. (1985) have recorded higher silica concentrations from Serengeti grasses than any previous studies of grasses. They also reported that the silica accumulation diminished from roots to leaves, in contrast to other studies, which report that leaves have more silica than roots (North American C4 grass *Calamovilfa longifolia*: Webb and Longstaffe 2002, bamboo *Phyllostachys heterocycla*: Lux et al. 2003). Paper I demonstrated that a grass diet wears teeth more than a browse diet, which supports the idea that grazing animals need more durable teeth and thus hypsodonty is beneficial for grazers.

It is also proposed that hypsodonty is related to overall aridity, because plants are

stiffer in arid environments and dust is more common (Baker et al. 1959, Janis and Fortelius 1988, Fortelius et al. 2002, Eronen et al. 2010a, Jardine et al. 2012, Fortelius et al. 2016). An experiment by Merceron et al. (2016) has demonstrated that dust does not affect the dietary signal of dental microwear textures. The sand grains with a mean diameter 233 μm that were used in paper I inflicted heavy damage to the tooth surface, although this sand was much coarser material than dust. Thus, hypsodont teeth are also beneficial for animals that eat in dusty and sandy areas. The most probable explanation is that both the physical properties of the plants and the exogenous material affected the evolution of hypsodonty (Janis and Fortelius 1988, Williams and Kay 2001).

Hypsodont and flat teeth with complex surface are a good indication of an animal that lives in an open grassland and consumes grasses (Damuth and Janis 2011, paper III). Warthog's hypsodont teeth have a flat occlusal relief and a complex occlusal surface and they live in a savanna environment and are mostly grazers (Ewer 1958, paper II). The similarity of the molars of *N. scotti*, *M. andrewsi* and the warthog indicates that the two Turkana Basin species were also open area grazers (paper III).

Lower hypsodonty in some species could be explained by the quality of the grasses (Janis and Fortelius 1988). Grasses in wetter areas, near rivers and in wooded areas might not be as abrasive as in arid open areas (Wilson et al. 1976, McNaughton et al. 1985), and the dust load would also be higher in the open arid areas. In addition, grasses have higher silica concentrations in heavily grazed areas (McNaughton et al. 1985). Such conditions would explain moderate hypsodonty in *Kolpochoerus* and *Hylochoerus*, as they have been proposed to prefer closed habitats near water sources (Kullmer 1999, Bishop et al. 2006).

5.4 How did the Plio-Pleistocene Turkana Basin suids respond to the changes in the environment? (papers II and III)

White (1995) tested if the speciation and extinction events of the Turkana Basin suids and hominins were initiated by climatic changes by studying their first and last appearance datums. He identified increased diversification and extinction rate between 2 and 3 Ma and a stronger pulse of speciation and extinction between 1.6 and 2 Ma without dramatic climatic oscillations.

Paper II shows that several suid genera were abundant in the same fossil localities in three time periods during the Plio-Pleistocene in the Turkana Basin. Around 4 to 3.5 Ma, the last nyanzachoeres and *Notochoerus euilus* were found at the same localities; during 3 to 2 Ma, *Notochoerus*, *Kolpochoerus* and *Metridiochoerus* were all present; and during 1.5 to 0.7 Ma, *Kolpochoerus* and *Metridiochoerus* were both abundant (paper II). The key adaptations and rise of new species of suids, especially grazing adapted forms, occurred during the last 5 Myr in the Turkana Basin. At the same time, C4 biomass was steadily increasing (Levin et al. 2011), which indicates an increase in the amount of grasses.

The first evidence of increased aridity and C4 biomass was recorded from 4.3 Ma (Wynn 2004, Liddy et al. 2016). However, the expansion of C4 plants and animals consuming them did not appear to be coincident with long-term aridification in the Turkana Basin (Blumenthal et al. 2017). The success of *Notochoerus* is most probably linked to the increase of grasses in the woodlands (Cerling et al. 2011). While *Notochoerus euilus* had

additional cusp pairs in its third molars, the molars were not extremely hypsodont. Grasses in woodland areas were possibly not as abrasive as in more arid open areas (Wilson et al. 1976, McNaughton et al. 1985). Thus, late nyanzachoeres and early notochoeres were able to increase grasses in their diet by increasing the chewing area of their molars.

Aridity punctuations occur around 3.58-3.35 Ma, 2.52-2 Ma, and 1.81-1.58 Ma (Wynn 2004). At the same time, woody cover was increasing from 5 Ma until 3.6 Ma and then decreased to its minimum to 1.87 Ma (Cerling et al. 2011). *Notochoerus scotti* appeared during the first aridity punctuation, and nyanzachoeres disappeared (paper II). The second aridity puncture occurred at the same time as the appearance of a large freshwater lake (Trauth et al. 2005), and *Kolpochoerus* and *Metridiochoerus* increased their relative abundances, while *N. euilus* disappeared. During the third aridity punctuation, *Metridiocheorus* started to dominate the suid record, and *N. scotti* disappeared (paper II). The appearances and disappearances of suid species during the aridity punctuations suggest that the arid time intervals might have been important in their evolution. *Notochoerus scotti* was probably a grazer (paper III). The aridity and the possible lack of quality food might have been a limiting factor for a large-sized grazing suid. The large size might have affected behaviour too; for example, extant warthogs use resting burrows where the temperature fluctuates less than outside (Bradley 1971). Similar behaviour would have been difficult for a larger suid. Although, larger size itself might be a good buffer against weather changes.

It is also notable that species that indicated similar dental topography in paper III were not dominant at the same time. Instead, they changed places: when *N. euilus* disappeared, *K. heseloni* started to be abundant; when *N. scotti* declined, *M. andrewsi* became the dominant suid (paper II).

6 Conclusions and directions for future

In this work, I have approached the peculiar case of suids that change from an omnivorous to grazing lifestyle in multiple lineages in eastern Africa during the Plio-Pleistocene. I have done so by 1. testing the dental wear of diets with different amounts of abrasives in a laboratory setting with a mechanical masticator, 2. analysing the abundances of the Turkana Basin suids in different time intervals in relation to changes in the climate and environment, and 3. identifying the relationship between diet and dental topography in present-day suids and applying the results to suid fossils.

I will summarize the main findings of this work by answering the questions presented in section 1.5:

1. Can we reproduce dental wear with a mechanical masticator and use it to analyse differences between diets?

- Paper I proved that it is possible to produce microwear on dental enamel in laboratory settings with a mechanical masticator, real teeth and diets. However, all diet groups produced scratch-dominated microwear pattern. In contrast, chewing in water without food items produced more pit-dominated pattern.

- The experiment with the mechanical masticator demonstrated that the grass diet wears teeth more than the browse diet does, although their microwear pattern on enamel

was similar in our experiment setup. Thus, the turnover rate of microwear patterns is higher with the grass diet than with the browse diet. Although the simplified laboratory setup could be the reason for the similar scratch-dominated microwear patterns in all diets, the results are a good reminder for the importance of multiproxy approach.

2. What causes the observed difference in dental wear between browse and graze diets?

- The experiment with the mechanical masticator did not produce significantly different microwear pattern between browse (lucerne) and graze diets. The reason might be either in the used simplified setup that does not take account meticulous chewing mechanics or in the food material that was pelleted food dissolved in water, and thus did not have the structure of a natural food material.

- The results suggest that phytoliths have important role in dental wear in the non-sandy diets in our experiment setup.

3. How much does grit impact dental wear?

- At least cattle and sheep have been demonstrated to ingest soil material either by accident or voluntarily to get minerals (Healy and Ludvig 1965, Mayland et al. 1977). In paper I sand grains (5 %, mean diameter 233 μm) were added to one of the tested diet groups. They inflicted heavy wearing on the teeth and larger pits on the enamel than other diets. While this result may be exaggerated by assuming animals would ingest that much sand, it does show that quartz particles wear teeth if they are consumed with the food items. More work on even smaller particle sized quartz (dust) is needed.

4. Did the Plio-Pleistocene suids of the Turkana Basin differ in their habitats and respective dietary preferences as they rose and fell in abundance during their history?

- The different lineages of the Turkana Basin suids peaked at different time intervals, which permitted several lineages to have similar adaptations. Conversely, *Kolpochoerus* and *Metridiochoerus* were both abundant from 1.9 to 0.7 Ma, which suggests differences in their ecological niches. In addition, the results from the dental topography study suggest that *K. heseloni* and *M. andrewsi* did not share similar diet.

- The extreme hypsodonty and horizodonty of the third molars developed in both *Notochoerus* and *Metridiochoerus* lineages. *Notochoerus scotti* and *Metridiochoerus andrewsi* also share similar dental topography with the present-day *Phacochoerus*. However, the species with extreme dental dimensions, *N. scotti* and *M. compactus*, never occurred at the same time.

- During the aridity punctuations suid lineages disappear and new ones rise to be abundant. Therefore, the aridity punctuations might have had significant impact on the relative abundances and evolution of the Turkana Basin suids.

5. Can we classify the diets of extant suids from patterns of their dental topography?

- The results suggest that dental topography analyses can be used as an accurate predictor not only for the three broad diet categories (grazer, mixed-feeder, browser), but also finer dietary categories such as frugivorous-dominated omnivore.

- Dental topography analyses (RFI, MSS, angularity, SHI, DNE, and OPC) were applied

to suids for the first time. The results revealed that the analyses could capture the relationship between dental topography and diet preferences in present-day suids. The extant warthog (*Phacochoerus*), the only dedicated grazer among the present-day suids, differed from the omnivorous suids (*Potamochoerus*, *Babyrousa* and *Sus*) and the herbivorous mixed-feeder *Hylochoerus* by all used analyses except DNE, which we think is highly dependent on the quality and processing of the 3D-meshes. Mixed-feeder *Hylochoerus* could be separated from the omnivorous suids by its higher MSS, higher RFI and greater SHI. Finally, among the omnivorous suids, the tropical forest suids that preferred fruits and tubers, *Potamochoerus* and *Babyrousa*, could be separated from the generalist *Sus* due to their lower OPC.

6. What was the diet of the Plio-Pleistocene Turkana Basin suids compared to the extant suids?

- The Turkana Basin suids resembled *Phacochoerus* the most due to their high complexity (OPC) and angularity in the dental topography analyses. This suggests that grass was part of their diet. *Notochoerus scotti* and *Metridiochoerus andrewsi* also had similar SHI and MSS suggesting that they were predominantly grazers like *Phacochoerus*. In contrast, *N. euilus* and *K. heseloni* had more similar MSS and SHI to that of the omnivorous present-day suids suggesting that their teeth had tools for the variety of food items found in their intermediate environment.

In the future, similar relative abundance and dental topography analyses could be performed on suids of the other parts of the Rift Valley and possibly other parts of Africa. This would obtain better resolution for temporal changes of the suid palaeoecology in Africa during the Plio-Pleistocene. The hypothesis that suids might have used forest corridors for moving between inland basins in wetter time periods, like suggested for hominins in Joordens et al. (2019), could be analysed with similar, but broader approach.

Mesowear analysis for suids could be developed from the 3D scans for the reconstruction of palaeoenvironments. Mesowear analysis is used for the reconstruction of palaeoenvironments, but suids have not contributed to those analyses because there has not been tailored mesowear analysis for suid teeth.

The body mass and variation in sizes of the Plio-Pleistocene suids could be examined in the future as those factors might affect feeding strategies. Only a few body mass estimations have been conducted for African Plio-Pleistocene suids (Pickford 2013, pers. comm. Juha Saarinen). It seems that Plio-Pleistocene suids tended to be larger compared to present-day suids. It is not certain, if the body masses grew steadily through the Plio-Pleistocene or if there were some time intervals when larger species appeared rapidly.

Finally, the role of fine-grained dust in dental wear should be tested as it is often hypothesised to be the driver for hypsodonty (Williams and Kay 2001, Mendoza and Palmqvist 2006, Damuth and Janis 2011). Fine-grained dust has not been tested in natural setup because controlling the dust is hard. Thus, mechanical masticator experiments with controlled fine-grained dust may be optimal. The wear potential of pure cellulose should also be tested because it is often stated that cellulose cannot scratch enamel (Danielson and Reinhard 1998) because it is not hard enough, but no long time chewing experiments have been conducted to test it.

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